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GENETICAL STUDIES ON ŒNOTHERA. IV

THE BEHAVIOR OF HYBRIDS BETWEEN *Œnothera biennis* AND *Œ. grandiflora* IN THE SECOND AND THIRD GENERATIONS[1]

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THOSE who have followed the reports of my genetical studies on *Œnothera* (Davis, '10, '11 and '12*a*) must have noted that I have obtained during the past four years a series of hybrids from the cross *grandiflora* × *biennis* with various points of strong resemblance to forms of *Œnothera Lamarckiana* De Vries. I say forms of *Œ. Lamarckiana* because it is, I think, clear (Davis '12*a*, p. 383) that this species has within itself a number of biotypes which, although in most respects essentially similar, differ from one another in the size of the petals, in the height of the stigma relative to the tips of the anthers, and, to a lesser degree, in some other characters. These biotypes may be segregated by critical selection and cultivation through pure lines and I venture to believe that the *Lamarckiana* of De Vries's cultures was less pure when he began his studies twenty-five years ago than it is to-day. At the present time a very large-flowered type (petals 4–4.5 cm. long) is generally thought

[1] An abstract of this paper was presented before the American Society of Naturalists at its meeting in Cleveland on January 2, 1913.

of when this plant is discussed. *Lamarckiana* then, like many species, has its minor strains which may be isolated.

Heribert-Nilsson ('12) in his recent extended analytical studies on *Œ. Lamarckiana* reaches the same conclusion that *Lamarckiana* is not a simple species but, on the contrary, polymorphic. His investigations are the first serious attempts to bring forward evidence that will explain the "mutants" and minor varieties as derivatives from a hybrid through the segregation and recombination of characters on Mendelian principles. These studies form a very important contribution to the research upon this interesting plant.

I have not as yet among my hybrids of *biennis* and *grandiflora* obtained any plant that matches in all respects any one of the biotypes of *Lamarckiana*. On the other hand, there is, I believe, no important character of taxonomic value presented by *Lamarckiana* through its various biotypes that has not appeared in some of my hybrids. I have, as it were, surrounded the group of *biotypes*, which we call the species *Lamarckiana*, with a circle of hybrids that in various characters agree with the plants that have come down to us through the cultures of De Vries. If the group of biotypes of *Lamarckiana* is enlarged to include certain of its so-called "mutants" the number of my hybrids with points of resemblance to this larger assemblage is correspondingly increased.

My studies have now reached a stage where I have data to present on the behavior of hybrids between *biennis* and *grandiflora* in the F_2 and F_3 generations. These later hybrids have a two-fold interest; first with respect to their possible interpretation in relation to Mendelian principles of inheritance, and second, with respect to the behavior of certain types in the F_2 generation, which types repeat in the F_3 the history of the F_1 parent hybrid in throwing the same marked variants, and thus exhibit a behavior similar to that of *Lamarckiana* when

in successive generations it produces a series of similar "mutants."

There has come to light during the past year a historical matter of interest which bears very directly on the problem of the origin of the *Lamarckiana* of De Vries's cultures. This is the determination of Lamarck's plant, *Œnothera Lamarckiana* Seringe (1828), grown in Paris at about 1796 or somewhat earlier, as a form of *Œ. grandiflora* Solander (1789) = *Œ. grandiflora* "Aiton." The evidence for this determination (see Davis, '12*b*) is very convincing and there can be, I think, no doubt but that De Vries ('01, Vol. I, pp. 316, 317) was mistaken when he identified the material of his cultures with the type specimen of *Œ. Lamarckiana* Seringe, the sheet upon which Lamarck (?1798) based his description in the Encyclopédie Méthodique Botanique. It should be remembered that Professor De Vries made this identification some years before the rediscovery of *Œ. grandiflora* at its original habitat in Alabama in 1904, and consequently before there was available our present information on this species.

Œnothera Lamarckiana Seringe (1828) now becomes a synonym of *Œ. grandiflora* Solander, described in Aiton's "Hortus Kewensis" (1789), and the material of De Vries's cultures can not bear the name *Lamarckiana* with Seringe as an authority. I have suggested, however, in the paper cited above (Davis, '12*b*, p. 530) that the plant of De Vries's cultures retain the name *Lamarckiana* to be written in the form *Œ. Lamarckiana* De Vries. A change of name for this plant would be most unfortunate, since it would result in endless confusion in the literature of experimental morphology. The evidence indicates that *Œ. Lamarckiana* De Vries has come to us as the product of the garden through a long history of cultivation and that its parentage is far from pure; in short, that it is of hybrid origin. As a garden plant we are seemingly justified in giving it the name *Œ. Lamarckiana* De Vries by Article 50 of the code

formulated by the International Botanical Congress held in Vienna in 1905.

The effect of the separation of *Œ. Lamarckiana* De Vries from Lamarck's plant of about 1796 is to make far more tangible the problem of its origin. In former papers in the NATURALIST (Davis, '11, p. 226; '12, p. 379) I have criticized adversely the attempts that have been made to place the appearance of *Lamarckiana* De Vries in Europe at dates previous to 1778 when *Œ. grandiflora* Solander was introduced at Kew. In a recent contribution Gates ('13, pp. 17–19) admits that the presence of *Lamarckiana* in Europe previous to 1760 is not established and thus abandons his former position when he sought to prove its very early introduction from America. With Lamarck's plant (*Œ. Lamarckiana* Seringe) removed from the discussion we are brought to periods where we may hope for more direct evidence on the history of *Lamarckiana* De Vries than that furnished by old accounts and figures. This matter will be further discussed at the end of this paper in the section entitled, "The Problem of the Origin of *Œ. Lamarckiana* De Vries."

The material of this paper will be arranged under the following headings: (1) F_3 Generations in the Family from the F_1 Hybrid 10.30*La*, (2) F_3 Generations in the Family from the F_1 Hybrid 10.30*Lb*, (3) Hybrids of *grandiflora B* × *biennis D* in the F_2 Generation, (4) A Discussion of the Behavior of the Hybrids in the Second and Third Generations with Reference to the Stability of Mendelian Factors, (5) The Habit of "Mutation" in *Œ. Lamarckiana* De Vries considered with Reference to the Behavior of the Hybrids between *biennis* and *grandiflora*, (6) The Problem of the Origin of *Œ. Lamarckiana* De Vries.

1. F_3 Generations in the Family from the F_1 Hybrid 10.30*La*

The F_1 hybrid plant designated 10.30*La* has already been described and figured (Davis, '11, pp. 211–213, Figs. 9, 10, 11), and a brief account of its F_2 generation was given in my last paper (Davis, '12*a*, pp. 410–413). The plant was the result of the cross *grandiflora B* × *biennis A*, the latter parent being a rather small-flowered race of *biennis* from Woods Hole, Massachusetts. The F_2 generation from 10.30*La* consisted of 1,451 plants, among which could be readily selected at an early stage of development a group of 141 rosettes much smaller than those constituting the mass of the culture and sharply distinguished by their strongly etiolated leaves of a narrower form. From these etiolated rosettes developed a class of dwarfs, the later foliage of which outgrew the etiolated peculiarities of the young plants and became green. The normal green rosettes constituting the mass of the culture presented a remarkable range of form, but inclined more towards the female parent of the cross, *grandiflora B*.

A large proportion of the plants, at maturity, were fairly close to the F_1 hybrid plant 10.30*La*, but there was presented a wide variation from this form with a markedly greater tendency towards the *grandiflora* parent type. Although the range of variation clearly indicated a process of segregation in this F_2 generation, it was a segregation modified by a general progressive advance in the size of the plant organs. Thus, with respect to flower size, the culture gave a large number of plants (about 50) with flowers as large as or larger than the *grandiflora* parent, while the smallest flowers represented were 2–4 times larger than those of the *biennis* parent. The leaves throughout the mass of the culture were, as a whole, larger than those of the parents of the cross and generally distinctly crinkled.

It should be recalled (see Davis, '12*a*, p. 412) that a

number of remarkable forms appeared in the F_2 culture in addition to the segregates, forms which no taxonomist would think of relating to either parent of the cross or to the F_1 hybrid plant 10.30*La*. Some of these forms were sterile, but the 141 peculiar dwarfs from etiolated rosettes and the extreme types showing progressive evolution were fertile, as was the culture, as a whole.

The problem which I outlined for study through the F_3 generation was two-fold: (1) Would extreme types of the F_2, such as the dwarfs, hold their characteristics, and (2) Would a selfed plant representative of the mass of the F_2 produce an F_3 progeny with points of similarity to the F_2 generation? If this proved true there would be presented a behavior analogous to that of *Lamarckiana*

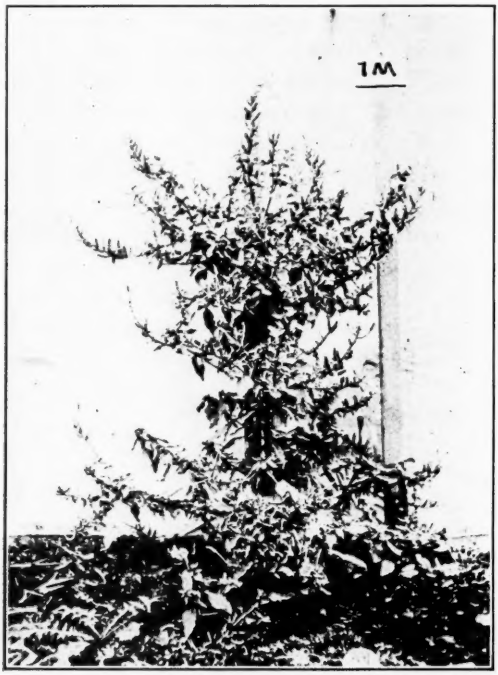


FIG. 1. Dwarf, 11.41*ra*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora* $B \times$ *biennis* A. This plant came from an etiolated rosette and shows the irregular branching characteristic of these dwarfs.

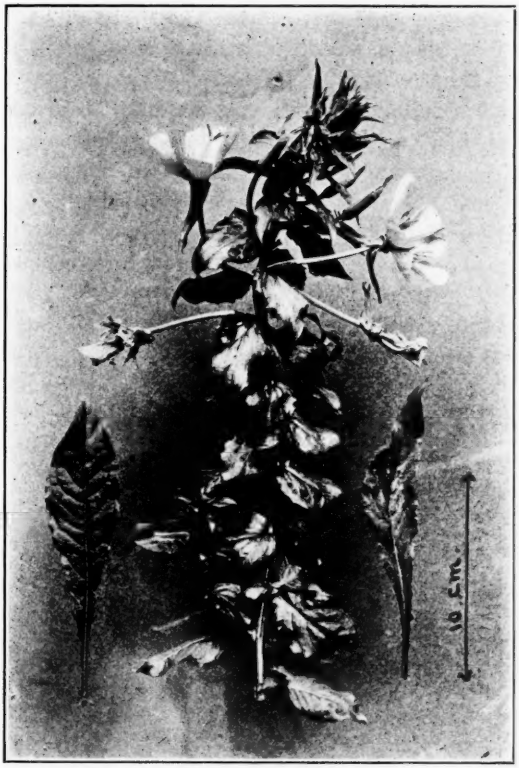


FIG. 2. Dwarf, 11.41*ra*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora B* × *biennis A*. The inflorescence and two leaves from the lower portion of the plant illustrate the varied forms of the leaves.

which throws off in successive generations marked variants which hold true when self-fertilized.

A plant, 11.41*ra*, was selected as being representative of the F_2 dwarfs from etiolated rosettes (Davis, '12*a*, p. 413) and, being selfed, became the parent of an F_3 generation (culture 12.53). The stunted growth and irregular branching characteristic of these dwarfs was well illustrated by this plant, 11.41*ra* (Fig. 1), as was also the varied form of the leaves (Fig. 2). The peculiarities of the etiolated rosettes from which the dwarfs come are well shown by the two plants at the bottom of Fig. 4.

From the F_2 dwarf, 11.41*ra*, 243 seeds, the contents of a single selfed capsule, were sown (culture 12.53). These produced 116 seedlings, the leaves of which, following the cotyledons were strongly etiolated in the lower half in the manner characteristic of these dwarfs; 69 rosettes were potted and carried to an advanced stage of development; 48 plants were brought to maturity. The rosettes were all etiolated, in some cases over three fourths of the basal portion of the leaves, in others somewhat less; the leaves were narrow and long-petioled. The F_3 generation (culture 12.53), from the F_2 dwarf, 11.41*ra*, was then absolutely true to the characters of the etiolated rosettes, one of which is shown in Fig. 4, 12.53*a*. The 48 plants brought to maturity presented the dwarf habit with ir-

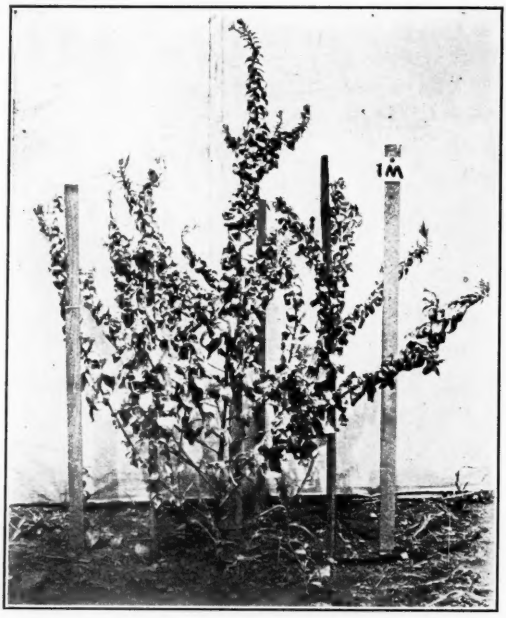


FIG. 3. A type, 11.41*c*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora* $B \times$ *biennis* A. This plant represented closely the character of the mass of the F_2 generation and was similar to the F_1 parent 10.30*La* except for a progressive advance in leaf and flower size.

regular branching and varied leaf form characteristic of the F_2 parent, 11.41*ra*; these plants also outgrew later the etiolated peculiarities of their rosettes. The flower size among these 48 plants of the F_3 varied greatly, a further point of similarity to the group of dwarfs in the F_2 generation. It appears then, as far as this culture in the F_3 gives evidence, that the dwarfs from etiolated

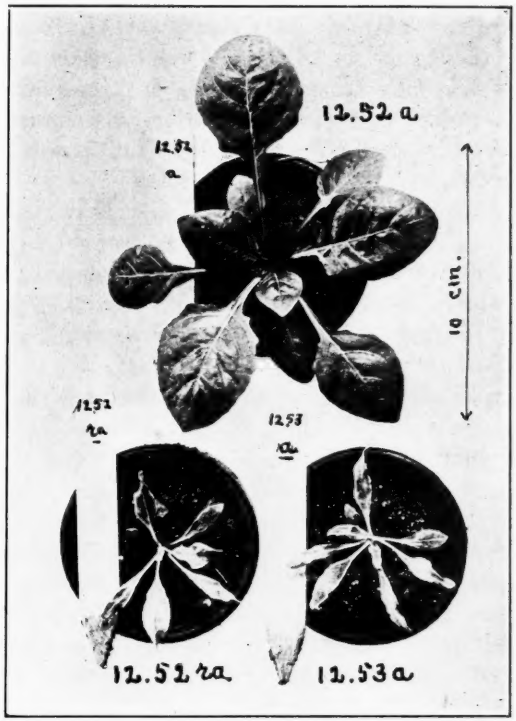


FIG. 4. 12.52*a* and 12.52*ra*, rosettes in the F_3 from the F_2 plant 11.41*c* (Fig. 3), the first, representative of the green rosettes constituting the mass of the culture, the second, one of 18 etiolated rosettes that developed into dwarfs. 12.53*a*, one of the etiolated rosettes in the F_3 from the F_2 dwarf 11.41*ra* (Figs. 1 and 2); it holds perfectly the characters of its F_2 parent, and is shown for comparison with 12.52*ra*.

rosettes in the F_2 generation constitute a group of plants very stable and perhaps homozygous with respect to their most striking peculiarities.

The second part of my study of this family concerned the behavior in the F_3 of a plant representative of the mass of the F_2 generation. The individual chosen, 11.41*c* (Davis, '12*a*, p. 412), was a large plant (Fig. 3) with long branches from the base and a foliage of conspicuously crinkled leaves. The type was represented by about 170 plants in the culture and, intergrading with other forms, stood close to the center around which the mass of the culture varied. This plant, 11.41*c*, was similar to the F_1 parent hybrid, 10.30*La*, except that it showed something of the general progressive advance throughout the F_2 generation in the broader and more crinkled leaves and in the somewhat larger flowers (petals 2.5 cm. long).

From the plant 11.41*c* an F_3 generation was grown (culture 12.52). There were sown 411 seeds, the contents of 3 selfed capsules and 285 rosettes developed. Among the seedlings 18 plants at once caught my attention as having etiolated leaves following the cotyledons. These 18 seedlings developed into small rosettes with narrow, strongly etiolated leaves, which could not be distinguished from the etiolated dwarfs that have been described above. The contrast between the green rosettes of this culture, 12.52, and these etiolated dwarfs, is illustrated in Fig. 4, which shows sister plants, 12.52*a* green and representative of the mass of the culture, and 12.52*ra* one of the 18 etiolated dwarf types. By the side of 12.52*ra*, for comparison (see Fig. 4), is shown one of the 48 etiolated dwarfs in culture 12.53, which, although an F_3 individual from 11.41*ra*, illustrates accurately the appearance of the etiolated dwarfs in the F_2 generation. It will be noted that the two dwarfs, 12.52*ra* and 12.53*a*, are of the same type.

The 18 etiolated rosettes of the F_3 culture 12.52 grew into dwarfs indistinguishable in all essentials from the 48 plants of the F_3 generation 12.53 and the 141 plants in the F_2 represented by 11.41*ra* (Figs. 1 and 2). They outgrew the etiolated condition of the younger stage, but re-

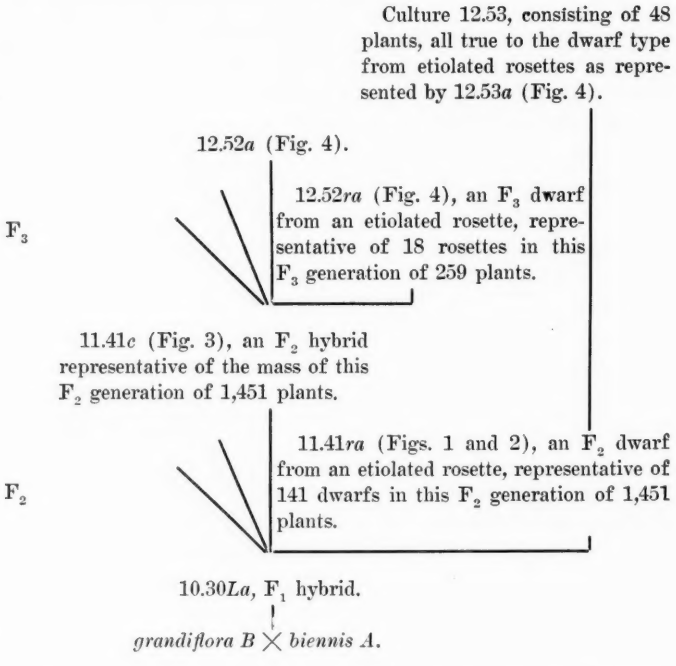
mained dwarfs, branching irregularly and presenting varied forms of leaves; there was also exhibited the same wide range of flower size. The evidence was then clear that in this family an F_2 plant of a type close to the mass of the F_2 culture could throw off in the F_3 the same class of dwarfs that appeared in the F_2 generation.

The normal green rosettes constituting the mass of the culture 12.52 (see Fig. 4, 12.52*a*) inclined strongly towards the *grandiflora* parent of the cross, but presented broader leaves not so strongly cut at the base. There was a wide range of variation among the rosettes, and forms appeared with narrow leaves which developed into plants with a foliage markedly different from the mass of the culture. The mass of the culture presented the same evidence of progressive evolution which was shown in the F_2 generation, *i. e.*, the leaves were large and crinkled as in the F_2 parent plant 11.41*c*, and there was likewise maintained the same advance in the size of the flowers, which ranged from types as large as or larger than the *grandiflora* parent to types as small as that of the F_1 hybrid 10.30*La*. In short, this F_3 generation, culture 12.52, from a plant 11.41*c*, fairly representative of the mass of the F_2, repeated the performance of the F_2 in exhibiting a large class of the same type of dwarf from etiolated rosettes and also repeated very much the same range of variation in leaf and flower characters shown by the F_2 generation. There was then presented a behavior closely parallel to that of *Lamarckiana* when it throws off in successive generations the same marked types of variants, which hold true.

Late in the season two plants were noted (12.52*fa* and 12.52*fb*) upon which a large number of flowers were 5-merous, *i. e.*, the flowers had 5 sepals, 5 petals, 10 stamens, and as far as noted 5 cells in the ovary. I am not aware that this character has before been noted in the genus *Œnothera*. These flowers were not restricted to particular branches and were found in the same inflorescence with normal flowers. The 5-merous flowers, were not ob-

served by me until October, too late in the season to self-pollinate with the hope of obtaining seed. Open-pollinated seed was, however, collected from these two plants and will be sown in the hope that this interesting sport may be followed in later generations.

The genealogy of the family from the F_1 hybrid 10.30*La*, in so far as it refers to the production of dwarfs, is presented in outline as follows:


Culture 12.53, consisting of 48 plants, all true to the dwarf type from etiolated rosettes as represented by 12.53a (Fig. 4).
12.52a (Fig. 4).
12.52ra (Fig. 4), an F3 dwarf from an etiolated rosette, representative of 18 rosettes in this F3 generation of 259 plants.
F3
11.41c (Fig. 3), an F2 hybrid representative of the mass of this F2 generation of 1,451 plants.
11.41ra (Figs. 1 and 2), an F2 dwarf from an etiolated rosette, representative of 141 dwarfs in this F2 generation of 1,451 plants.
F2
10.30La, F1 hybrid.
grandiflora B × biennis A.

2. F_3 Generations in the Family from the F_1 Hybrid 10.30*Lb*

The F_1 hybrid designated 10.30*Lb* was a sister plant to 10.30*La* and, therefore, also the product of the cross *grandiflora B* × *biennis A*. It has been described and figured in the earlier paper (Davis, '11, pp. 213–216, Figs. 12, 13 and 14), and a brief account of its F_2 generation

will be found in my last contribution (Davis, '12*a*, pp. 413–415). From the F_2 generation of 992 rosettes, culture 11.42, a group of 147 were sharply distinguished by their uniformly small size and narrow leaves. These developed into a class of very remarkable dwarf plants (Davis, '12*a*, p. 415, 11.42*r*) which at maturity were from 3–4 dm. high, rarely branched, and bore medium-sized flowers (Fig. 5). The leaves of the rosettes and mature plants were fully green; there was no etiolation so characteristic of the group of dwarfs from the sister F_1 hybrid 10.30*La*. The character of the young dwarf rosettes is shown in Fig. 7 and Fig. 9, 12.59*a*, in comparison with rosettes (shown above) similar to forms representative of the mass of the culture.

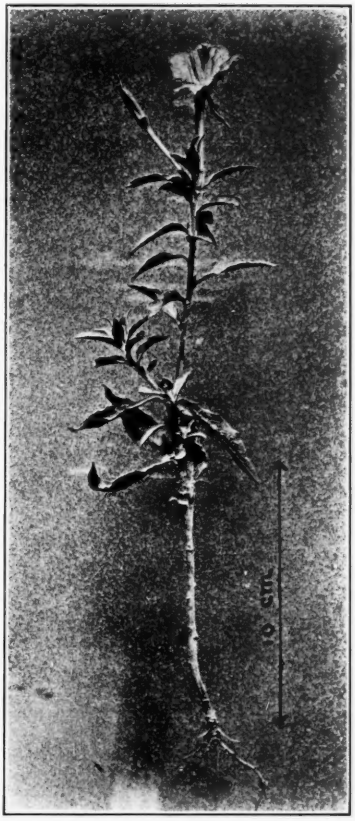


FIG. 5. Dwarf, 11.42*r*, in the F_2 from the F_1 plant 10.30 *Lb*, hybrid of *grandiflora B* × *biennis A*. This plant came from a rosette similar to that shown in Fig. 7, 12.59*a*.

The rosettes constituting the mass of the culture exhibited a wide range of form with the extremes approaching the rosettes of the *biennis* and *grandiflora* parents; there was not shown a clearly defined tendency towards either parent of the cross. From these rosettes a much more varied culture developed than the F_2 generation from the plant 10.30*La*.

There was more evidence of segregation towards the respective parents, but the same progressive advance in flower size. Many plants bore flowers as large as or larger than those of the *grandiflora* parent, while no plant presented flowers as small as those of the *biennis* parent. The foliage was extremely varied, ranging from lanceolate leaves to broadly elliptical or ovate leaves with well-defined crinkles.

A larger number of remarkable forms appeared in this culture, 11.42 (see Davis, '12*a*, p. 415), than in the one from the plant 10.30*La*, forms that would rank as types specifically distinct from either parent of the cross and from the F_1 hybrid plant 10.30*Lb*. Among these we shall refer to (1) the dwarf type 11.42*r* (Fig. 5), (2) a small-leaved type 11.42*f* (Fig. 6), (3) a large-flowered type with large crinkled leaves 11.42*g* (Fig. 8), rather common and fairly representative of the mass of the culture, (4) a medium-flowered type remarkable for its broad-much-crinkled leaves 11.42*l* (Fig. 14), and (5) a plant with very narrow leaves and very small flowers, anthers sterile 11.42*j* (Fig. 15).

The same problem lay before me in the study of the F_3 generations from these types in the F_2 of the plant 10.30*Lb*, as in the family which has just been described from the sister plant 10.30*La*. Would the extreme types such as the dwarfs hold their characters, thus proving to be homozygous, and would selfed plants more or less representative of the mass of the F_2 repeat in their F_3 generations something of the history of the F_2?

Of the 147 dwarf rosettes in the F_2 from 10.30*Lb* there were brought to maturity 90 plants. These constituted, as stated above, a very uniform group with characters well shown in Fig. 5. One of these, 11.42*ra*, was selected and selfed to become the parent of an F_3 generation. The contents of one capsule, 196 very small seeds, were sown and gave culture 12.59, comprising 66 rosettes, all similar and dwarf. One of these rosettes is shown in

Fig. 7 and Fig. 9, 12.59*a*, and it should be noted that the specimen is not a seedling, but a half-grown rosette comparable in point of age to the large rosettes (shown above) which represent closely the normal form and size. The dwarfs are delicate plants, very sensitive to drought, and I was able to bring only 46 individuals to maturity. These proved to be in all respects similar to the dwarfs of the F_2 generation, except that they were even smaller in stature and flower size; this further dwarfing was, however, probably due to less favorable cultivation. From the behavior of this F_3 we may, I believe, safely conclude that the dwarfs of the F_2, representing an extreme type, are stable, or homozygous, with respect to their most important characteristics.

There will now be described the F_3 generation from a small-leaved plant, 11.42*f* (Fig. 6), about 1 m. high, with

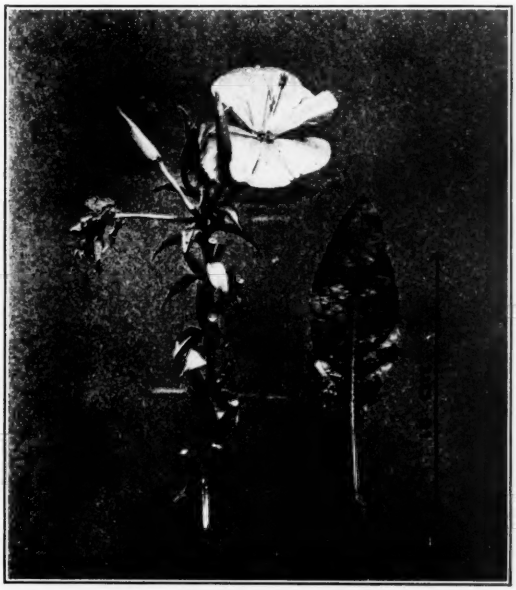


FIG. 6. A type, 11.42*f*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora* $B \times$ *biennis* *A*. A form characterized by small leaves, medium-sized flowers, and large capsules.

medium-sized flowers and large capsules (3.3 cm. long). This type (Davis, '12*a*, p. 415, 11.42*f*) was represented by several plants in the F_2 from 10.30*Lb*. It illustrated an extreme combination of small leaves with large capsules,

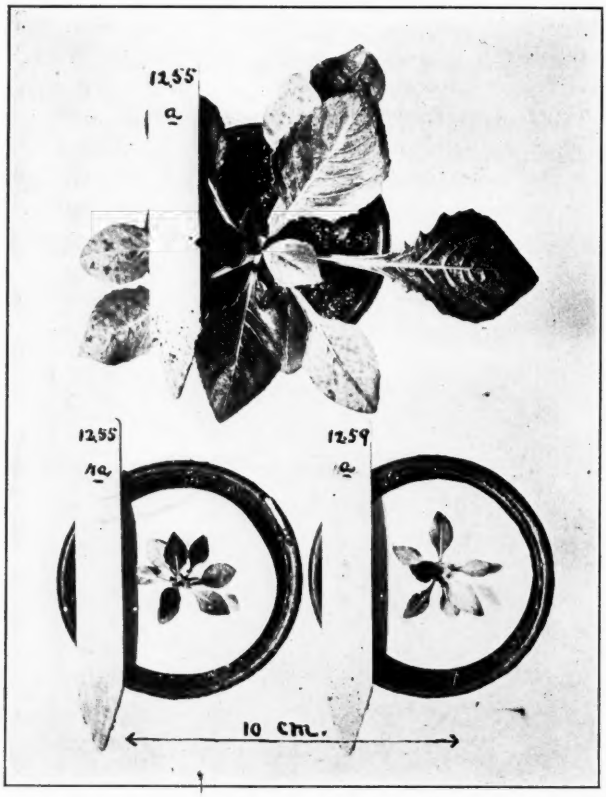


FIG. 7. Rosettes in the F_3: 12.55*a* representative of the mass of the culture from the F_2 plant 11.42*f* (Fig. 6); 12.55*ra* a sister rosette, one of 8 dwarfs in the same culture; 12.59*a* a rosette from a plant similar to 11.42*r* (Fig. 5).

but must not be regarded as representing a class since its characters intergraded through numbers of plants into the mass of the culture. The contents of one selfed capsule, 219 seeds, were sown as culture 12.55; these produced 75 seedlings from which 62 rosettes developed.

From the mass of rosettes with characters as illustrated in Fig. 7, 12.55*a*, a group of 8 dwarfs (Fig. 7, 12.55*ra*) was quickly recognized. One can hardly imagine a much sharper contrast between rosettes in the same culture than is shown in this illustration (Fig. 7, 12.55*ra* compared with 12.55*a*). By the side of the dwarf 12.55*ra* is a rosette, 12.59*a*, of the F_3 from one of the dwarfs of the F_2, 11.42*ra* (similar to Fig. 5). A comparison will show how perfectly the F_2 type 11.42*f* (Fig. 6) has repeated the behavior of its parent hybrid F_1 plant 10.30*Lb* in throwing off a class of similar dwarfs. The 8 dwarfs of the culture 12.55 were set out under conditions ill-suited to their constitution and I had great difficulty in saving 5 plants from a period of drought. These are now in the hot house, where it is hoped that they may be brought to maturity.[2]

The normal rosettes of the F_3 culture 12.55, excluding the 8 dwarfs described above, developed a fairly uniform set of plants which at maturity exhibited a foliage of broader and more crinkled leaves than those of the F_2 parent hybrid 11.42*f*. This progressive advance in foliage was also supplemented by a greater vigor and size of the plants, although the flowers remained without marked change. Summarizing the behavior of the F_2 plant 11.42*f* in the F_3 generation, the most striking points were the repetition of the behavior of the F_1 parent hybrid 10.30*Lb* in throwing off the same types of dwarfs, and a much greater uniformity among the normal plants with apparent advance in leaf size and vegetative vigor.

The next form to be considered is a plant, 11.42*g*, which was fairly representative of the mass of the F_2 generation from 10.30*Lb*. This plant (Davis, '12*a*, p. 415, 11.42*g*) was 1.5 m. high and characterized by large flowers (petals about 4 cm. long) and large crinkled leaves (Fig. 8). It was a type rather common and intergrading with other forms of the culture. It exhibited a decided progressive advance in flower and leaf size over the F_1

[2] Of the 5 dwarfs 3 are now (June 1, 1913) almost full grown and true to the type.

parent plant 10.30*Lb*, but stood close to the center around which the mass of the F_2 culture varied.

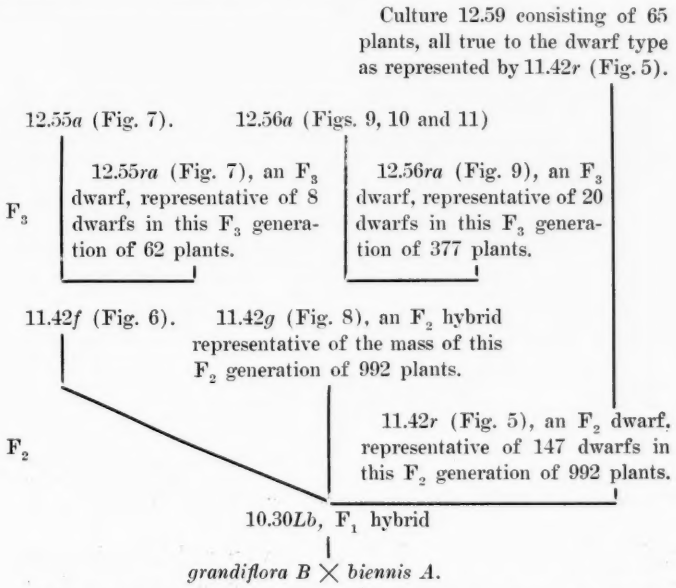
From this plant, 11.42*g* (Fig. 8), the contents of two

FIG. 8. A type, 11.42*g*, representative of the mass of the F_2 generation from the F_1 plant 10.30*Lb*, hybrid of *grandiflora* $B \times$ *biennis* A. A form characterized by large, crinkled leaves and large flowers (petals 4 cm. long).

capsules, about 900 seeds, were sown (culture 12.56) and 377 rosettes developed. Among the rosettes a group of 20 dwarfs very shortly defined itself. The characters of the dwarfs are illustrated in Fig. 9, 12.56*ra*, where they may be compared with those of a normal rosette, 12.56*a*, shown above. The same sort of contrast is here exhibited as that illustrated by Fig. 7 for the culture from 11.42*f*. By the side of the dwarf 12.56*ra* is again figured the

rosette 12.59*a* (compare Fig. 9 with Fig. 7) of the F_3 from one of the dwarfs in the F_2, 11.42*ra* (similar to Fig. 5). Figs. 7 and 9 then illustrate the same behavior, in the first case that of the F_2 plant 11.42*f*, and in the second case that of the F_2 sister plant 11.42*g*, and both plants have produced a class of dwarfs similar to that which appeared in the F_2 11.42*r*, the type shown in Fig. 5. I had the same difficulty with the 20 dwarfs from 11.42*g* as with the 8 from 11.42*f* and was only able to save 7 plants from a period of drought. These at the present writing are also in the hothouse, where they bid fair to reach maturity.[3]

An outline of the genealogy of the sets of dwarfs produced by the family from the F_1 hybrid 10.30*Lb* will make clearer its complications. The important feature is of course the close parallelism of this history with the behavior of *Lamarckiana* when it produces in successive generations a marked variant that breeds true.


Culture 12.59 consisting of 65 plants, all true to the dwarf type as represented by 11.42r (Fig. 5).
12.55a (Fig. 7).
12.56a (Figs. 9, 10 and 11)
F3
12.55ra (Fig. 7), an F3 dwarf, representative of 8 dwarfs in this F3 generation of 62 plants.
12.56ra (Fig. 9), an F3 dwarf, representative of 20 dwarfs in this F3 generation of 377 plants.
11.42f (Fig. 6).
11.42g (Fig. 8), an F2 hybrid representative of the mass of this F2 generation of 992 plants.
F2
11.42r (Fig. 5), an F2 dwarf, representative of 147 dwarfs in this F2 generation of 992 plants.
10.30Lb, F1 hybrid
grandiflora B × biennis A.

[3] Of the 7 dwarfs 4 are now (June 1, 1913) almost full grown and true to the type.

Of the 357 normal green rosettes in culture 12.56 from 11.42*g*, 128 plants were set out and brought to maturity. A single interesting rosette with leaves sharply streaked with white failed to live. The rosettes consisted of unusually broad, ovate or elliptical leaves, loosely arranged (see Fig. 9, 12.56*a*). The group of plants at maturity

FIG. 9. Rosettes in the F_3: 12.56*a* representative of the mass of the culture from the F_2 plant 11.42*g* (Fig. 8); 12.56*ra* a sister rosette, one of 20 dwarfs in the same culture; 12.59*a* a rosette from a plant similar to 11.42*r* (Fig. 5).

exhibited a range of variation in flower and leaf size, but on the whole was remarkably uniform except for the plant 12.56*x* to be described later.

The type characteristic of this group (culture 12.56) is one of the most interesting among my hybrids and will be

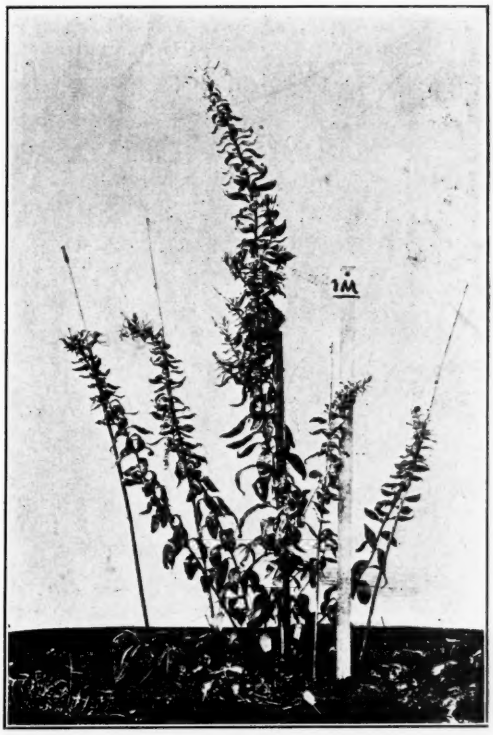


FIG. 10. Mature plant, 12.56*a*, from the rosette 12.56*a* (Fig. 9), representative of the mass of the F_2 generation from the F_2 hybrid 11.42*g* (Fig. 8). A form remarkable for the size and thickness of the leaves, size of flowers and general vigor.

briefly described. It is a large plant, 1.5–2 m. high, with long branches from the base (Fig. 10), stem green above, reddish below, leaves much larger and thicker than in *grandiflora,* and strongly crinkled. Inflorescence (Fig. 11) *grandiflora*-like, very dense on the main branches, bracts persistent. Buds 8–9 cm. long, cone circular in section, sepals green, their tips attenuate. Petals about

4 cm. long. Stigma 5–8 mm. above the tips of the anthers. Capsules 2.8 cm. long.

Although this type presented many of the peculiarities of the *grandiflora* parent, there was evident a remarkable

FIG. 11. Flowering side branch of the F_3 hybrid 12.56*a* (Fig. 10), showing the *grandiflora*-like inflorescence and broad crinkled bracts. At the right is a leaf from the lower portion of the main stem.

degree of progressive evolution in the size and thickness of the leaves, size of the flowers, and general vigor. These progressive advances introduce characteristics of

Lamarckiana and make this type a very favorable one for back crossing with certain races of *biennis* which in certain respects (*e. g.*, stem coloration, rosette characters, etc.) are closer to *Lamarckiana*. Such a back cross was made last summer with *biennis D* and should result in a further advance towards the synthesis of *Lamarckiana*-like hybrids between *grandiflora* and forms of *biennis*.

The single plant, designated 12.56*x* in the culture de-

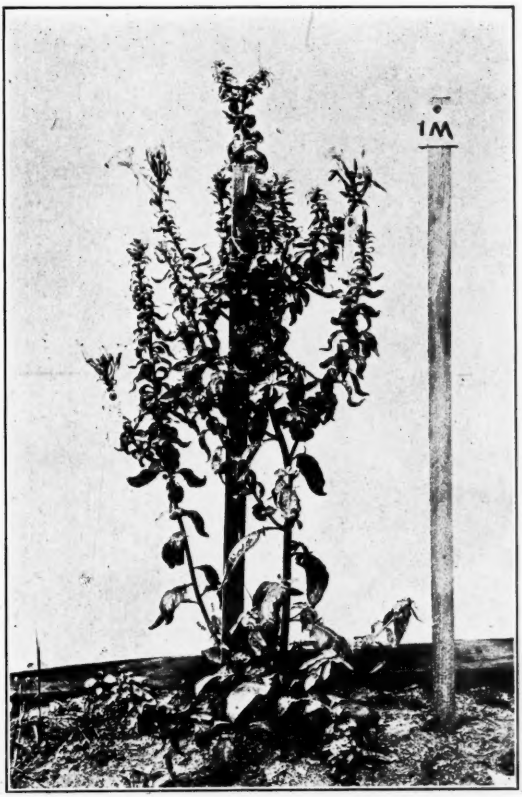


FIG. 12. Mature plant, 12.56*x*, a remarkable type represented by a single individual in the F_3 from the F_2 hybrid 11.42*g* (Fig. 8). A form distinguished by its stocky habit and very large thick leaves. The plant had at least 21 chromosomes, the triploid number.

scribed above, presented characters that distinguished it from the mass in much the same way that *gigas* is distinguished from *Lamarckiana*. In the rosette stage the plant was marked because of the exceptional thickness and large size of the leaves. The mature plant, somewhat more than 1 m. high (Fig. 12), was much shorter

FIG. 13. Flowering side shoot of the F_3 hybrid 12.56*x* (Fig. 12), showing the four-angled buds, and dense inflorescence, flat-topped because of the short internodes. At the right is a leaf from the lower portion of the main stem.

and more stocky (*gigas*-like) than the average of the culture; the leaves were even thicker. The inflorescence (Fig. 13) was more dense because of the shorter internodes so that the top appeared flattened as in *gigas*.

The buds, 8–9 cm. long, presented a stouter cone, 4-angled, and the sepal tips were less attenuate and thicker. The petals were about 4 cm. long, the hypanthium was shorter, and the stigma lobes, 4–6 mm. above the tips of the anthers, were thicker than in the type representative of the mass of the culture. The capsules, 1.8 cm. long, were shorter and stouter. So many of these points of difference suggest the characteristics of *gigas* that it was not surprising to find the chromosome count to be above 14, the normal diploid number for *Œnothera*. It is difficult to determine the exact number, but from counts made this spring at the growing points of seedlings from this plant I am certain that the chromosome count is at least as high as 21, the triploid number. It will be remembered that the triploid number has been determined by both Miss Lutz ('12) and Stomps ('12) for "mutants" derived from *lata* and *Lamarckiana* to which Stomps has given the name *semi-gigas*. We have then in this plant (12.56*x*) a variant from the parent hybrid which probably corresponds closely to the "triploid mutants" of *Lamarckiana* or its derivatives.

There will now be briefly described the F_3 generation from a type 11.42*l*, represented by a single plant in the F_2 from 10.30*Lb* (Davis, '12*a*, p. 415, 11.42*l*). This plant, about 1 m. high, was remarkable for its broad, entire, much-crinkled leaves (Fig. 14); the flowers were medium-sized (petals 2 cm. long). The contents of two capsules, 222 seeds, were sown, from which 117 plants were obtained and brought to maturity (culture 12.58). The mass of the rosettes consisted of broad elliptical leaves, crinkled and loosely arranged. Several rosettes were *grandiflora*-like, intergrading, however, with the mass, and 8 presented a long narrow form of leaf. The culture at maturity was very well graded from plants 1.6 m. high, with flowers as large as those of *grandiflora* (petals 3.5 cm. long) to plants the counterpart of the F_2 parent hybrid 11.42*l*. The foliage of the culture as a whole continued the progressive advance of 11.42*l* as shown by

larger leaves which were more strongly crinkled. The plants from the 8 rosettes with narrow leaves also had at

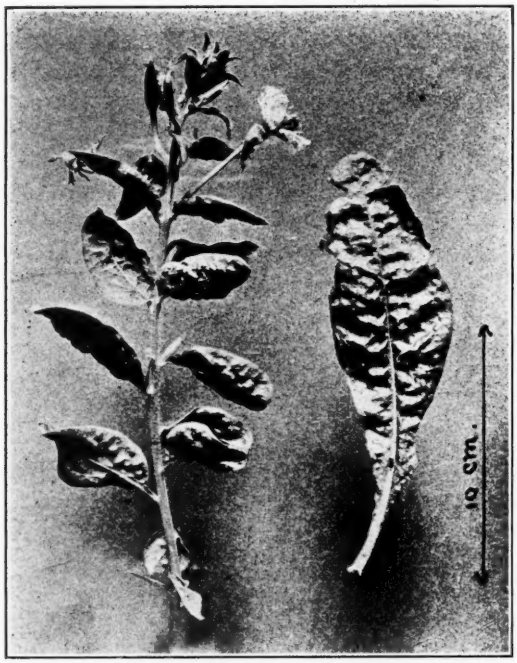


FIG. 14. A type, 11.42*l*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora* $B \times$ *biennis* A, represented by a single plant. A form characterized by its broad, entire, much crinkled leaves and medium-sized flowers (petals 2 cm. long).

maturity smaller and narrower leaves; the flowers were medium-sized (petals 2.5 cm. long). They constituted a clearly defined group but could not be called dwarfs. It is interesting to note that an F_2 type so clearly defined as 11.42*l* may, nevertheless, be strongly heterozygous and consequently may be very far from representing a stable segregate in the F_2.

A remarkable plant, 11.42*j*, appeared in the F_2 from 10.30*Lb* (Davis, '12*a*, p. 415, 11.42*j*) which in habit and

foliage agreed very closely with the "mutant," *Œnothera elliptica* obtained by De Vries ('01, vol. I, pp. 280–284) from *Lamarckiana*. This plant, 7 dm. high, developed from a rosette with narrow leaves and at maturity presented a foliage of very narrow leaves well illustrated in

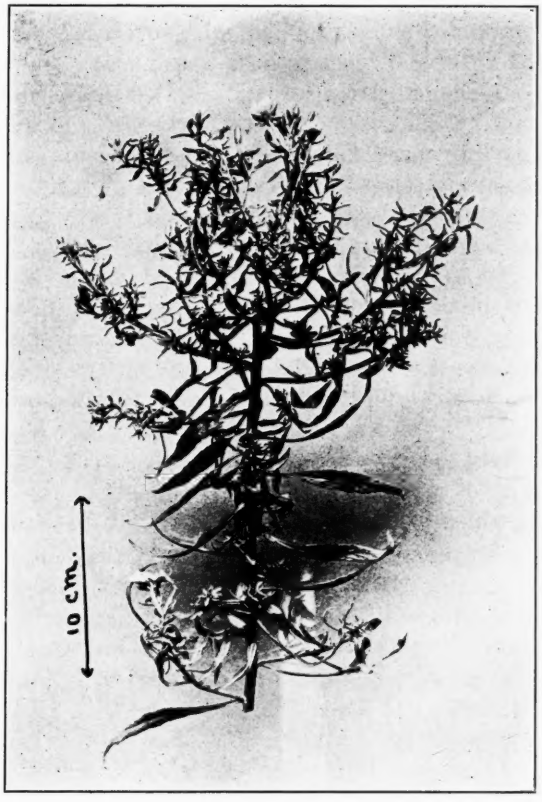


FIG. 15. A type, 11.42*j*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*, represented by a single plant. A remarkable form with a foliage of very narrow leaves, and with very small flowers (petals 6 mm. long), anthers sterile. This plant in its habit and foliage matched closely De Vries's "mutant" *Œnothera elliptica*.

Fig. 15, which shows the top of the main stem. The

flowers, however, were very small (petals 6 mm. long) and the anthers as far as observed were completely sterile. Since this plant apparently could not be selfed, I pollinated it from a large sister plant of the F_2 with *grandiflora*-like flowers. The result was 154 seeds from several capsules which gave 46 plants in the F_3 generation (culture 12.57). Of the rosettes, 40 proved to be large-leaved, exhibiting much variation, but with several plants similar to *grandiflora;* 6 rosettes bore long narrow leaves.

From the 40 large-leaved rosettes there developed plants 1.2–1.5 m. high with a foliage of crinkled leaves, and medium-sized flowers (petals 2–2.5 cm. long). Of the 6 narrow-leaved rosettes, 5 developed plants which agreed with the "*elliptica*" type and 1 became a broad-leaved form similar to the 40 described above. The 41 large-leaved plants of the culture evidently took their characteristics largely from the pollen parent of the cross and represented something of a blend. I am at a loss to account for the five individuals of the "*elliptica*" type unless they came from apogamously formed seed. The "*elliptica*" type has since appeared in other F_2 generations from the cross *grandiflora* × *biennis,* and it appears to be a not uncommon expression of one of the extreme forms which may be thrown in the F_2 of this cross.

(*To be continued*)

THE INFLUENCE OF PROTRACTED AND INTERMITTENT FASTING UPON GROWTH

DR. SERGIUS MORGULIS

In an earlier paper on inanition[1] I pointed out the significance of the period following a prolonged fast in investigating the problem of growth. Prolonged starvation—notwithstanding the exhaustion which it produces—seems to exercise a rejuvenating effect upon the assimilative capacity of the organism, which builds itself up again with surprising rapidity as soon as feeding is resumed. It was also shown there, that the increase in weight of the animal does not necessarily correspond to the quantity of ingested food, being somewhat greater than the latter, which is due to absorption of water from the surroundings. Whereas inanition causes a relatively greater loss of dry substance than of water, it was found that "the effect of resumed feeding (upon the salamander) is to increase the water content more relatively than the dry substance" (p. 213).

Since those results were published I had an opportunity of collecting more material bearing upon this topic. The experiments were made with the salamander *Triton cristatus,* and strengthen my former observations on *Diemyctylus viridescens.* In the subjoined Table *A* the data as to the weight of nine salamanders with the exact amounts of food taken during 7 to 14 days after starvation are summarized. The renewal of feeding after several weeks of privation does not generally proceed smoothly, the animals either taking sick or refusing the food, hence the relapses with the diminution of the body weight which may be seen occasionally throughout the table.

[1] Morgulis, S., "Studies of Inanition in its Bearing upon the Problem of Growth," I, *Arch. f. Entw.-Mech.,* Bd. 32, 169–268, 3 plates, 1911.

That the rate of growth is independent of the amount of nutrition is revealed by these experiments in a striking manner; they show rather the reverse, namely, the utilization of the food by the organism according to the need of its tissues and cells. The impulse to grow plays the leading part here, not the quantity of food brought into the digestive organs, and in this respect the growth after starvation has much in common with embryonic growth.

TABLE A

No.	1		2		3		4		5		6		7		8		9	
Days of Feeding	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.
1	0.631	.0450	0.631	.1020	0.755	.1125	1.067	.0580	0.882	.0480	0.889	.0870	0.826	.0920	0.887	.1300	0.821	.0843
2	0.679	.0368	0.749	.0790	0.865	.0565	1.093	.0620	0.917	.0610	1.077	.0870	0.967	.1460	1.084	.1300	0.929	.0736
3	0.729	.0535	0.872	.0490	0.959	.0590	1.102	.0910	1.025	.0610	0.977	.0870	1.169	.1460	0.978	.1300	0.969	.0631
4	0.780	.1215	0.897	.0590	0.973	.0590	1.207	.0570	0.988	.0625	0.937	.1450	1.122	.1270	0.909	.1300	0.969	.0953
5	0.922	.0920	0.977	.0520	0.923	.0525	1.231	.0655	1.041	.0690	1.109	.1450	1.206	.1270	0.909	.1300	1.058	.0662
6	1.077	.0920	0.977	.0520	0.923	.0525	1.251	.0690	1.104	.0540	0.887	.1210	1.146	.1270	0.864	.1520	1.055	.0990
7	0.941	.0920	0.961	.0725	0.919	.0740	1.251	.0690	1.104	.0540	0.978	.0890	1.140	.1270	1.063	.1070	1.000	.0856
8	0.898	.0920	1.001	.1100	1.011	.0930	1.308	.0960	1.037	.1000	1.020	.0890	1.090		1.146	.1070	1.064	.0998
10	0.898	.0920	1.001	.0770	1.011	.1170	1.308	.0800	1.037	.0980	1.020	.0890	1.090		1.146		1.064	
12	0.898	.0920	0.937	.0700	1.107	.0665	1.308	.1070	1.037	.0870	1.020	.0890	1.090		1.146		1.064	
13	0.898	.0920	0.937	.0700	1.107	.0665	1.351	.1030	1.157	.0780	1.020	.0890	1.090		1.146		1.064	
14	0.898	.0920	0.937	.1580	1.107	.1270	1.351	.1030	1.157	.0780	1.020	.0890	1.090		1.146		1.064	
15	1.011	.0920	1.227	.1580	1.227	.1270	1.399	.1030	1.263	.0780	1.120	.0890	1.243		1.200		1.211	

Food offers merely a greater or less scope to the inherent growth-tendency of the organism, and, like so many other factors, may either increase or decrease its effect. It is possible that the reduction in size of the cells, or rather the diminished ratio between cell-body and nucleus, has something to do with the observed processes of intense growth, and that the rejuvenescence of the organism is analogous to the condition in the embryo, where the cell-body is likewise small in relation to its nucleus. There is certainly more than mere superficial resemblance between the two phenomena of growth from the point of view of the protein metabolism. Already in the eighties

Kahan[2] observed that after seventeen days of inanition (when the body had suffered a loss of 31 per cent.) rabbits gained 56 per cent. in weight on a diet even less sufficient than that, which could just maintain them in a state of equilibrium under normal conditions. The retention of protein by the cells, as their principal building material, is greater than usual, and along with it goes the retention of water.

If the growth of the body as regards weight corresponded to the amount of food taken for that period of time, then the coefficient of growth should be equal, $G/F=1$. According as to whether a larger or smaller portion of the food is transformed into body substance, *i. e.*, participates in growth, the coefficient ought to vary from 0 to 1. Furthermore, when the increase in weight of the animal exceeds the quantity of ingested food, the coefficient will rise above 1. In the following Table B we give the records of the body weights for consecutive days, the amount of food ingested and the corresponding coefficient of growth of four animals.

TABLE B

ANIMAL 1

Date	Nov. 3	December						Total for 7 Days
		22	23	24	25	26	27	29	
Body weight in grm.	.910	.631	.679	.729	.780	.922	1.077	.898	
Difference in weight		−30.6%	+.048	+.050	+.051	+.142	+.155	—	+.267
Amount of food given (in grm.) on previous day			.0450	.0368	.0535	.1215	.0920	—	.3488
Ratio between increase in weight and amount of food			1.07	1.36	.95	1.17	1.68	—	.77

[2] Kahan, J. A., "Der Einfluss des Hungerns auf das Körpergewicht bei der Auffütterung von Tieren mit einer beschränkten Nahrungsmenge nach einem überstandenen Hunger," *Russ. Medizin*, Nr. 17–19, 1885.

ANIMAL 2

Date	Nov. 8	January								Total for 7 Days
		3	4	5	6	7	8	9	10	
Body weight in grm....	.892	.631	.749	.872	.897	.977	?	.961	1.001	
Difference in weight....		−29.3%	+.118	+.123	+.025	+.080	?	−.016 (?)	+.040	+.370
Amount of food given (in grm.) on previous day.....			.1020	.0790	.0490	.0590	.0520	——	.0725	.4125
Ratio between increase in weight and amount of food.....			1.16	1.56	.51	1.36	?	?	.56	.89

ANIMAL 3

Date	Nov. 8	January								Total for 7 days
		3	4	5	6	7	8	9	10	
Body weight in grm....	1.064	.755	.865	.959	.973	.923	—	.919	1.011	
Difference in weight....		−29.0%	+.110	+.094	+.014	−.050	—	−.004	+.092	+.256
Amount of food given (in grm.) on previous day.....			.1125	.0565	.0590	——	.0525	——	.0740	.3545
Ratio between increase in weight and amount of food.....			.98	1.67	.024	?	?	?	1.28	.72

ANIMAL 5

Date	Nov. 14	January								Total for 7 Days
		2	3	4	5	6	7	8	9	
Body weight in grm....	1.140	.882	.917	1.025	.988	1.041	1.104	—	1.037	
Difference in weight....		−22.7%	+.035	+.108	−.037	+.053	+.063	—	−.067	+.155
Amount of food given (in grm.) on previous day.....			.0480	.0610	——	.0625	.0690	.0540	——	.2945
Ratio between increase in weight and amount of food.....			.73	.177	——	.85	.91	?	?	.53

The animals were weighed both before and immediately after feeding, so that the amount of food consumed could be ascertained accurately by subtracting the former weight from the latter. After twenty-four hours the animals were weighed again, the difference between this weight and that of the previous day giving the growth for twenty-four hours. In some cases the increase is only a fraction of the quantity of food which the animals received; not infrequently, however, it has been even greater than that quantity. In the case of the four salamanders recorded above there are ten out of eighteen determinations, which show an excess of growth over the amount of ingested food. We find that the coefficient of growth never falls below 0.5 (the one instance where it is only 0.24 is obviously accidental); in other words, as regards weight the increase of the body is never equal to less than one half of the quantity of ingested material, and the average coefficient for all four animals for a seven-day period of renewed feeding is 0.73. This fact is particularly significant when we compare it with the condition found in continually fed specimens. In the case of other four control salamanders it was found that the coefficient of growth was only 0.26, *i. e.*, only about 26 per cent. of the food had gone to the building up of the body substance.

When the growth occasioned by a return to a normal diet after a protracted starvation is studied from the point of view of the body dimensions instead of the body weight, it appears that it is exceedingly slow during the first two weeks, showing that during that time primarily the internal organs undergo reparation, the enlargement of the musculature and of the skeleton ensuing subsequently.

Salamanders fed intermittently did not become as heavy nor as large as the control specimens; that is to say, their growth has been retarded from the point of view of both weight and size. The coincidence of the results of measuring both weight and length of the body

strengthens our conclusion that frequently repeated starvation affects unfavorably the vitality of the organism. The conclusion concurs with that of Kahan,[3] who subjected pigeons two or three times to hunger, feeding them very abundantly in the periods between, and found that their power of resistance declines with each new experience of starvation.

> Der nach vorhergegangenem Hungern bei unbeschränkter Nahrungsaufnahme aufgefütterte Organismus zeigt die Folgen der früheren Nahrungsentziehung, . . . und bei wiederholter Nahrungsentziehung rascher verfällt, als der gesunde (p. 277).

Seland[4] experimenting with chickens got quite different results. He allowed his birds to reach a state of equilibrium in body weight, when food was withdrawn for periods of one to two days, and then they were again fed. He discovered that the periodically fasting birds grew heavier than the control, although they were actually getting less food. According to von Seland, the increase is not caused by a deposit of fat, but by an accumulation of albuminous material, and the periodic fasting has the effect of making the body heavier, stronger and more solid. Von Seland's assertion, however, regarding the increase in quantity of the albuminous substances lacks the proof of chemical analysis.

We saw in the foregoing that after a period of protracted starvation, when about one fourth of the body weight has been lost, growth is very intense and the per cent. of the consumed food which becomes converted into the substance of the organism is nearly three times as large as in the continually fed salamanders. The impulse to grow determines the degree of utilization of the nutriment, the rate of growth being regulated by the particular state of the cells of the organism, which in turn is probably occasioned by the relation of the nucleus to the

[3] Kahan, J. A., "Mit Auffütterung abwechselnde akute experimentelle Inanition," *St.-Petersburger med. Wochenschr.*, Nr. 30, 275–277, 1886.

[4] V. Seland, "Ueber die Nachwirkung der Nahrungsentziehung auf die Ernährung," *Biol. Centralbl.*, Bd. 7, 145–158, 184–192, 214–224, 246–256, 271–281, 1887.

cell-body. We shall attempt now to demonstrate this point further by comparing the results obtained for long periods with differently nourished animals. The data which are given in the subjoined tables are so arranged that the number of times when either the starved or the periodically fasting salamanders received food is just one half of the number of feedings of the control specimens for some definite length of time. We take the *number* of feedings which could be obtained from the individual records as indicating the approximate amount of consumed food, since the actual quantities—except in a few instances—have not been measured directly. It is clear, of course, that animals fed *ad libitum* do not always take the same quantity of food, nor is it likely that different animals consume each similar amounts, but in the run of weeks it may be expected that the positive and negative variations will compensate for each other. We may, therefore, accept the *number* of times at which the animals received food as a measure for the *total quantity* of food consumed during a certain period. Furthermore, to make the weights of the different animals comparable with one another they have been computed on the assumption that the initial weight of all animals was one gram.

In Table *C* we have the data of four groups of starved salamanders and of their corresponding controls. The first two groups, each comprising four individuals, are compared at the end of 112 days, during which period the control specimens were fed 96 times, while the others (after 7–8 weeks of complete inanition) were fed 48 times. The ratio between the number of feedings being $1 \div 0.5$, it follows that by the end of 112 days the control animals have probably consumed twice as much food as the starved animals. The final body weight at the close of this period was 3.823 g. and 4.265 g. (1st group), and 3.092 g. and 3.694 g. (2d group), respectively. Taking the mean of these two groups, we get $1 \div 1.165$ as the ratio between the final weights, and $1 \div 2.45$ as the ratio between the daily increase in the control and starved

animals. Examining the data of the third and fourth groups where in the course of 84 days the control specimens were fed 72 times and the starved ones only 36 times we encounter practically the same result.

TABLE C

	Group	Control Animals (*A*)	Animals Fed after Protracted Starvation (*B*)	Ratio Between *A* and *B* (*A* = 1)
Number of feedings	i	96	48	1 ÷ 0.5
	ii	96	48	1 ÷ 0.5
	iii	72	36	1 ÷ 0.5
	iv	72	36	1 ÷ 0.5
Body weight (Initial wt. = 1 gr.)	i	3.823	4.265	1 ÷ 1.116
	ii	3.092	3.694	1 ÷ 1.195
	iii	2.557	2.170	1 ÷ 0.849
	iv	3.040	2.635	1 ÷ 0.867
Daily increase in body weight	i	0.029	0.068	1 ÷ 2.345
	ii	0.022	0.056	1 ÷ 2.545
	iii	0.022	0.033	1 ÷ 1.500
	iv	0.028	0.046	1 ÷ 1.643

The fact that in the case of these last two groups the starved individuals have not reached the same weight as the corresponding controls, whereas in the former two groups they even became by one-sixth heavier than the controls, must be attributed to the shorter duration of the feeding-up of these animals. We find thus that a fasting experience enables the organism to attain almost the same weight (or even a greater weight) which animals that did not have such an experience attain, upon half the quantity of their food supply, because the rate of growth after starvation is considerably greater.

We may proceed now in a similar fashion to compare the effect of continual and of intermittent feeding upon the growth of the body. These data are recorded in Table *D*, and are likewise calculated for an initial weight of one gram. The ratio between the number of feedings of these two kinds of animals being 1 ÷ 0.5, the respective body-weights have not become 0.5 of that of the control specimens, but 0.57–0.81; in other words, the intermittently fed animals have increased somewhat more than

the control animals would have done with the same quantity of food. Taking the average for all four groups together, we find that the intermittently fed specimens with one half the amount of food reach a little over two thirds of the body weight of the continually fed ones.

TABLE D

	Group	Control Animals (*A*)	Periodically Fasting Animals (*C*)	Ratio Between *A* and *C* (*A* = 1)
Number of feedings	i	120	60	1 ÷ 0.5
	ii	120	60	1 ÷ 0.5
	iii	120	60	1 ÷ 0.5
	iv	108	54	1 ÷ 0.5
Body weight (Initial wt. = 1 gr.)	i	4.395	2.520	1 ÷ 0.573
	ii	3.550	2.885	1 ÷ 0.813
	iii	3.520	2.490	1 ÷ 0.708
	iv	3.616	2.501	1 ÷ 0.692
Daily increase in body weight	i	0.028	0.025	1 ÷ 0.893
	ii	0.022	0.032	1 ÷ 1.455
	iii	0.021	0.025	1 ÷ 1.191
	iv	0.024	0.028	1 ÷ 1.167

Assuming the values for the normally fed animals equal to 1, we may sum up the results of our comparison of the growth in weight of continually fed individuals (*a*) and those starved (*b*) or intermittently fasting (*c*) in the following formulæ:

a	*b*	*c*	
1	0.5	0.5	Quantity of food.
1	2.01	1.18	Daily increase in weight.
1	1.01	0.70	Final body weight.

The results of the above study are obviously at variance with those of von Seland who found that his periodically fasting birds have been faring best. This difference in our results may, of course, be accounted for by the circumstance that the periods of fasting of my salamanders have been rather long (one to three weeks; also in Kahan's experiments the periods were from one and a half to two weeks) whereas von Seland's chickens have never fasted more than 12 to 48 hours at any time.

Why does the intermittent feeding produce such an inhibiting effect upon the growth of the body in weight? Before attempting to answer this question it should be recalled that these animals utilize a larger portion of their food in building up their tissues than normally fed salamanders do, the rate of their growth being likewise about one fifth greater. We also pointed out that the animals remained smaller in size and lighter in weight than the controls. We meet, thus, in the case of the periodically starved salamanders two contrary phenomena: on the one hand, we observed and directly measured on a number of individuals their deficient growth; on the other hand, we found that the growth activity has not been impaired, but even somewhat greater than in the case of the control Tritons. In the paper, already referred to in the beginning of this article, I showed that the water content of the organism increases 4 per cent. when salamanders are returned to a normal diet after protracted starvation. The water content probably comes back to the natural level when the animals have again reached their normal state. In the case of the intermittently fasting salamanders this may not happen, if the fast is repeated before the effect of the preceding inanition has been overcome. If we recall that the per cent. of water in the organism of starved individuals is also somewhat higher than the usual (by 1.5 per cent.) it becomes quite probable that water may be accumulating in the tissues of intermittently starved specimens to the extent of being a hindrance to their growth.

Acute hunger has an entirely different effect. It may even exhaust the organism for a time, but so long as degeneration has not set in—degenerative changes appear generally in the advanced stages of starvation—inanition may produce an invigorating influence upon the organism, which has its parallel in the embryonic growth only. The temporary relief which the organs of digestion get may contribute much towards improving their capacity, but the resulting rejuvenation of the organism is a com-

posite effect of the activity of all its cells. The chief reason for the revitalization of the organism is in the enhanced need of the cells for nourishment. The cells become "avaricious," if we may say so, and the increased proportion of the nucleus in the cell organization may perhaps in a measure be responsible for that.

From all that has preceded the conclusion can be drawn that periodic starvation is more detrimental to the organism than acute starvation followed by a liberal supply of food. In the former case the individual remains below the level of the normally fed animals; in the latter case, on the contrary, provided the inanition has not been carried too far, the restorative process may go even beyond the limit attainable under normal conditions. From the viewpoint of practical application this conclusion is evidently of importance, suggesting to those who have made the problem of social welfare their own the dangers to the health and vigor of mankind which lurk in the more commonly occurring underfeeding and chronic starvation, especially of the young and growing generation.

CAMBRIAN HOLOTHURIANS[1]

AUSTIN H. CLARK

Preface.—In a recent number of *Science*[2] Dr. Hubert Lyman Clark published a most interesting and valuable summary of the literature on the fossil remains of the Holothuroidea, accompanied by critical remarks. The greater part of his paper is devoted to a consideration of Dr. Charles D. Walcott's contribution to the knowledge of Cambrian geology and paleontology in which there are described as holothurians, under the new generic names *Eldonia, Laggania, Louisella* and *Mackenzia,* four new forms from the Middle Cambrian of British Columbia.[3]

Dr. Clark reaches the conclusion that *Laggania* can not positively be assigned to any invertebrate phylum, for he sees "nothing beyond the probable form of the body, and the terminal mouth, to suggest a holothurian, and these characters are equally suggestive of actinians;" *Louisella* he does not believe is a holothurian, though he can offer no suggestion as to its proper systematic position; *Mackenzia* he does not consider a holothurian; he hints that it may be an actinian, though he hastens to emphasize the fact that he does not positively make that assertion; *Eldonia* he is sure is not a holothurian, but he does not place it in any phylum.

To sum up Dr. Clark's criticism, he is sure that none of the four genera established by Dr. Walcott really belong to the Holothuroidea, but he is quite unable to suggest a more logical resting place for any of them.

[1] Published by permission of the secretary of the Smithsonian Institution who, however, does not hold himself responsible for any of the views expressed.

[2] *Science*, Vol. 35 (N. S.), No. 894 (February 16, 1912), p. 274.

[3] Smithsonian Miscellaneous Collections, Vol. 57, No. 3, pp. 41–58.

Dr. Clark remarks that in Fig. 2 on plate 13 (representing *Mackenzia costalis*) "the terminal mouth surrounded by a jointed or notched ring is distinctly shown; in the specimen I was unable to make out these points satisfactorily"; I can personally vouch for the presence of the "notched ring"; but after the specimen was photographed Dr. Walcott tells me that it was subjected to an acid bath in order to remove a deposit of calcite, and while it was in that bath the ring seems to have disappeared.

Dr. Clark laments that "if *Eldonia* is a holothurian, it becomes virtually impossible to define the class except in terms of the alimentary canal; indeed, if *Eldonia* is a holothurian, the echinoderms themselves can be defined in no other terms, for *Eldonia* lacks every single character which justifies the customary view that holothurians are echinoderms." I can not agree that *Eldonia* lacks every characteristic echinodermal character; but even if it did and we were forced to define the class Holothuroidea on the basis of the digestive tube the Holothuroidea would merely be brought into line with very many of the other animal groups. I would like to see Dr. Clark draw up a definition which would successfully differentiate the Trichoptera from the Lepidoptera, or the Orthoptera from the Neuroptera, or a definition which would include all the members of the Diptera, but exclude all other insects. The more we learn about the various types of animals the more it is impressed upon us that the dividing lines between them are purely arbitrary, and that there is a fundamental unity covering the whole field of zoölogy.

Introduction.—My study of the specimens upon which these new genera and species were based was entirely independent of that made by Dr. Walcott, and, on account of our entirely different previous training, I approached the problems presented in an entirely different way. Excepting *Eldonia,* I did not examine any of the genera in detail until after his paper was in press. After its publi-

cation the bearing of these new genera from the Cambrian upon certain phases of marine biology, especially on the probable age of the deep-sea fauna, led me to examine all of them with the greatest care in order to determine to my complete satisfaction whether the classification made by Dr. Walcott was beyond doubt justified by the available facts.

Dr. Clark and I examined the material together during a visit which he made to Washington; but we did not discuss the classification or the systematic position of the genera.

After the publication of Dr. Clark's article, as my examination of the material had led me to conclusions quite different from those at which he had arrived, it seemed advisable to put on record the results of my studies so that those to whom the material is not accessible may have, in addition to the published figures, which are wonderfully good and leave little to be desired, the conclusions of three entirely independent investigators, each with a very different previous training, and each entirely uninfluenced by the conclusions arrived at by the others.

Before taking up the discussion of these forms in detail it is advisable to give a brief outline of the general principles of deduction by which my conclusions regarding them have been reached.

The characters by which animals are identified are of two classes, the fundamental, or characters of prime systematic importance, and the correlative, or characters of prime practical importance, though often of no systematic importance whatever.

In the exceedingly rapid work, often under the most unfavorable conditions, demanded in the identification of organisms brought up by the dredge at sea one has no chance to look for fundamental characters. The general shape of the organisms, coupled with a few other obvious features, alone are depended upon. Thus a shell with a more or less polished surface and perfect bilateral symmetry is at once known to be a brachiopod, regardless of

whether it possesses a stalk or not; a soft and flabby, more or less shiny, tubular object, with or without body processes, is at once identified as a holothurian, no matter whether tentacles are visible or not, and quite regardless of its symmetry. In deep-sea work one soon gets to know the representatives of the various phyla by characters never mentioned in systematic treatises, and never even dreamed of by the laboratory student; yet the identification by these characters after practise is quite as sure as the identification by the features of real classificatory significance.

The identification of many fossils calls for essentially the same mental processes as the rapid identification of animals brought up by the dredge; one must be prepared to grasp at once the salient correlative features if the fundamental characters are obscured. Unfortunately this method of work has often yielded deplorable results when applied by paleontologists unacquainted with the practical side of the work of the marine biologist; but this is no reason why it should not lead to perfectly reliable conclusions when logically applied.

The chief of the correlative characters in any group of animals is the general body form taken in connection with the size. Thus in differentiating echinoderms from other organisms at sea we rely entirely upon size and shape; there is no time to look for radial symmetry; we probably take this in subconsciously, though it may be to a large extent mentally ignored.

When any member of a group of animals adopts a mode of life entirely different from that of all the other members of the same group we must be prepared to encounter extraordinary, sudden and unexpected changes in its organization which are not connected with the more usual type of organization by any intermediates; and it must be remembered that such changes affect first of all the general body form. Among such animals we almost always find the group characters developed in a most erratic manner; some structures will be very highly spe-

cialized, sometimes specialized far beyond what is seen in any other member of the group, while others will be in a very rudimentary or primitive state of development, or even absent altogether.

The echinoderms differ very abruptly from the crustacean line of descent from which they took their origin and, similarly, each echinoderm class differs very abruptly from all the others. We see in all the echinoderms to-day most perplexing combinations of primitive and highly specialized characters associated in all sorts of ways, and this leads us naturally to the assumption that there was no definite intergrade between the echinoderms and the barnacles, but that the former sprang from the latter or, more strictly speaking, from the same phylogenetic line which may be traced by easy stages to the latter, by a broad saltation in which the assumption of the free habit and the correlated assumption of pentaradiate symmetry combined to make the existence of intergrading forms impossible, while at the same time it resulted in the formation by the echinoderms, at the very moment of their origin, of two widely diverse stocks, the heteroradiate (including the Pelmatozoa, the Echinoidea and the Holothuroidea) and the astroradiate (including the Asteroidea and the Ophiuroidea) between which there are, and can be, no intergrading forms.

Thus in dealing with the echinoderms we must be ever on the alert to detect sudden saltations. We must also be prepared to eliminate from our minds all ideas of hypothetical ancestors from which all echinoderms are commonly supposed to have been derived, but which probably never existed; and, along with the hypothetical ancestor myth, to banish from our thoughts all ideas of fundamental echinodermal structures, equally non-existent. No echinodermal structure is of such fundamental importance in the economy of the animals that it can not be either profoundly modified or even dispensed with altogether under special conditions, reverting to a type more or less characteristic of some other phylum. The

pentaradiate symmetry is often brought forward as a character of the highest importance; but it is the result not of a class peculiarity, but of simple mechanics; the somatic divisions in the echinoderms are marked by lines of weakness; hence the divisions of the body must be uneven in number, so that no line of weakness will go straight through the body, thus subjecting the animal to danger through a shearing strain; when the somatic divisions are by lines of extra strength, as in the cœlenterates, the divisions are always equal, as in this case the continuation of a line of strength directly across the body gives added rigidity.

We know enough about organic life at the present day to be somewhat sceptical when new phyla are proposed to include problematical forms. If we can not allocate an animal on the basis of some supposedly fundamental character, or if it falls on the basis of a single character in a phylum from all the groups in which it differs in all the others, we ignore that character entirely and take up another. In every group each character has a definite and restricted application, beyond the limits of which it is quite valueless. The echinoderms are commonly said to be pentaradiate, and the great majority certainly are; but certain genera, entirely or in part, possess three, four (like most medusæ), six, seven, eight or ten rays; we recognize them as echinoderms just the same. Specimens of the genus *Limnocnida* are commonly pentaradiate; but we instantly recognize them not as echinoderms, but as hydromedusæ. The echinoderms we say have abundant calcareous deposits in the skin, and often also in the deeper parts of the body; the genus *Pelagothuria* has no trace of any calcareous deposits whatever, but no one doubts that it is an echinoderm.

These few obvious cases are selected from an almost unlimited choice; they show conclusively that any character, no matter how fundamental it may be, may suddenly become quite worthless, forcing us to depend entirely upon other characters which in other cases are

more or less ignored. Thus, to take two instances from the fossil crinoids, in the genus *Marsupites* the only feature which can possibly give a clew to its true affinities is the arm structure, which is that of an ordinary comatulid; and in the allied genus *Uintacrinus* the arm and pinnule structure alone are found to be reliable.

Eldonia.—In *Eldonia* there are only two structures upon which we can hope to base our deductions concerning its systematic position: (1) the bell-like general shape, and (2) the coiled digestive tube with two tentacle clusters at the anterior end.

1. The bell-like shape suggests the cœlenterates, and such forms as *Trochosphæra* or trochophore larvæ.

The highly specialized digestive tube at once negatives the supposition that *Eldonia* may be a cœlenterate.

Trochosphæra has a general form and an internal structure which is certainly suggestive of *Eldonia;* but there are many reasons why it is not possible to connect the two. In the first place there is the question of animal mechanics; the size of the members of each group of animals is limited by physical and mechanical considerations due to the requirements of fundamental structure, etc. Thus we do not find butterflies as large as ordinary birds, nor cetaceans so small as the average fish; their structure is not adaptable to the limitations imposed by such sizes. *Trochosphæra* is surrounded by a band of cilia, just below which is the mouth, and below that another band of cilia. Ciliated bands do not transform into broad body fringes such as we see in *Eldonia;* they are more or less uncertain structures, and are present as ciliated bands, or are absent altogether. *Trochosphæra* has a powerful retractor muscle attached to the posterior portion of the alimentary canal; powerful retractor muscles are a feature of all the rotifers; there is no trace of any retractor muscle in *Eldonia.*

In *Trochosphæra,* and in the so-called trochophore larvæ, the anus opens at the pole determined by the ciliated band as the equator, while the mouth is just below

the chief ciliated band. In *Eldonia* the mouth is the more central, and there appears to be a possibility that the anus is on the dorsal surface above the fringed border. The ciliated bands of *Trochosphæra* have a very definite connection with the mouth, a connection not evident between the fringed border of *Eldonia* and the mouth, the relationships in the latter being almost exactly like the relationships between the digestive tube and the expanded brim in such holothurians as *Euphronides tanneri.* Although the superficial resemblance between *Eldonia* and *Trochosphæra* (including trochophore larvæ) is certainly striking, I can not see the slightest reason for connecting the two; the relation between them is precisely similar to that between certain of the pteropods and the nautilus, which, on account of their remarkable similarity, were for a long while placed in the same genus.

2. Certain "worms" have a digestive system suggesting that of *Eldonia;* but such worms are never provided with oral tentacles, possessing instead a tough protrusible proboscis; nor do they ever have the digestive tube differentiated as in *Eldonia;* nor do they ever have the body of a type which, on account of the structure of the body wall and the general internal anatomy, particularly the type of muscular investment, could by any stretch of the imagination be supposed to assume a bell-like form.

Certain heteroradiate echinoderms, as some holothurians belonging to the family Elpidiidæ, a few echinoids, and the (recent) endocyclic crinoids, have a digestive tube resembling very closely that of *Eldonia,* and in the holothurians there are always tentacles about its anterior end. Moreover, in many of the Elpidiidæ, as, for instance, in *Euphronides tanneri,* the body is entirely surrounded by a broad brim with marginal lappets, just as it is in *Eldonia.*

Judging from all the evidence which we have—and the specimens of *Eldonia* are among the most wonderfully preserved fossils which have ever come to light—*Eldonia*

can be nothing else than a heteroradiate echinoderm, and among the heteroradiate echinoderms a holothurian, in which class it comes nearest to certain of the Elpidiidæ.

Affinities of Eldonia.—In *Eldonia* the body is medusa-like, circular, bordered with a broad *Euphronides*-like brim of uniform width; the mouth and anus are near together, the mouth being nearer the center; the general configuration of the digestive system is very similar to that seen in the endocyclic crinoids; there are two large many-branched tentacles, one on either side of the mouth.

Eldonia seems to me to be a pelagic derivative from some elpidiid type; the body has shortened so that the mouth and anus have become closely approximated; the brim surrounding the body has become laterally extended and uniformly developed, so that a swimming bell has resulted. *Eldonia* is therefore an elpidiid holothurian which has become flattened dorsoventrally and at the same time laterally expanded into a circular form resembling that of the medusæ.

We are familiar with just such a transformation in the echinoids; *Dendraster, Echinarachnius, Arachnoides,* etc., are flattened, circular and disk-like, though derived from ovoid, globular or more or less spherical types. In these the flattening has been in the direction of the radial symmetry so that the oral pole is at or near the center of one surface and the aboral pole at or near the center of the other. In *Eldonia* the flattening has possibly, though not certainly, been in a plane at right angles to this so that the oral pole is at one edge of the circular disk and the aboral pole at the other. This is only a slight advance over the conditions seen in *Benthodytes typicus,* so that it need occasion no surprise.

The reduction of the number of tentacles in *Eldonia* to two possibly indicates a suppression of three of the radial systems, leaving only two of the original five. Many of the crinoids show a more or less complete reduction of two or three of the radial systems; indeed, in *Tetracrinus* one is invariably absent.

In certain forms among the Comasteridæ, as, for instance, in *Comatula micraster,* ambulacral grooves, nerves and tentacles may be entirely absent from six out of the ten arms, or from three out of the five rays, leaving, as in *Eldonia,* only two of the original five divisions functioning normally, and these two may be three times as large as the others.

If we can assume that the two tentacles of *Eldonia* indicate a suppression of three of the original five radial systems, or a carrying out to completion of the condition already far advanced in many of the Elpidiidæ, a reasonable explanation of the structure of *Eldonia* becomes a relatively simple matter.

If we take a form like *Scytoplanes typicus* or *Euphronides tanneri* and shorten the body so as to bring the mouth and anus near together, giving the digestive tube exactly the same shape that it assumes in the so-called endocyclic crinoids, the two radial muscles would form a circular band of concentric muscle fibers just beyond the enteric canal, exactly as we see them in *Eldonia.*

Ordinarily among the echinoderms the mouth is at one pole of the radial symmetry and the anus is at the other. In the recent crinoids the anus has become entirely dissociated from the aboral radial pole and has migrated to a position near the mouth. It is thus evident that the connection between the anus and the aboral pole is not absolutely unchangeable.

The water vascular system centers, in all echinoderms, in a ring about the œsophagus, from which (usually) five radial canals are given off. How then can we account for the small central ring in the center of *Eldonia,* far removed from the mouth? The first question to be answered is whether the arrangement of the water vascular system about the mouth is really fundamental, or whether it is merely a matter of mechanical convenience when the mouth happens to be, as it usually is, at or near one of the apices of the pentamerous symmetry.

Now among the crinoids there are two families, the

Comasteridæ and the Uintacrinidæ, in which the mouth, instead of being as usual in the center of the ventral surface of the disk, is lateral, situated typically on the very edge of the ventral surface of the disk, between the bases of two of the arm groups. In these families the tubes of the water vascular system, above which ambulacral grooves usually, though not always, run, instead of converging in five large vessels to the circumoral ring lead from the arms to a large trunk vessel which runs around the periphery of the disk with the anal tube instead of the mouth as its center. This large peripheral ring, is interrupted posteriorly, and the mouth passes through it anteriorly; but it indicates a tendency for the water vascular system to transform from a ring about the mouth to a ring about the anal tube, or more correctly, into a ring about the ventral pole of the body regardless of the position of the mouth. In this connection it would be interesting to determine if in the Comasteridæ the so-called stone canals were confined to the circumoral ring, or if they showed a tendency to migrate secondarily along the peripheral water tube.

With the assumption by *Eldonia* of the circular form and the spiral digestive tube the muscles assumed a concentric arrangement. Probably at the same time the water tubes, following the course of the muscles, also attained the form of a peripheral canal, after the same manner as we see almost consummated in the Comasteridæ. The peripheral water tubes in *Eldonia* serve largely as braces to bind the animal together, just as they serve as braces in the marginal brim of *Euphronides tanneri*. This function would, for mechanical reasons, induce a diminution in the diameter of the central ring, in order that they might function to the best advantage; but the muscular ring, in order to preserve a maximum availability for expansion and contraction, would remain with the greatest possible diameter. Thus we should theoretically reach a condition precisely like that seen in *Eldonia;* a very large concentric muscular ring, and a

very small, also concentric, apical water vascular ring with exceedingly long tubes reaching out into the marginal tube feet, fused together into a broad and uniform marginal brim.

In *Eldonia* the radial canals so-called are the canals of the podia transformed into a system of braces, exactly as they are transformed into a system of braces in *Euphronides tanneri, Benthodytes typica,* and many similar forms; in these species, which live supported upon ooze and have developed a broad brim about their body so that they will not sink into it, the ring canal of the water vascular system retains its original position about the œsophagus, while in *Eldonia,* which floats free in the water, and possesses a medusoid body form, the canals have become enormously elongated and of uniform length all around, serving as body supports (like the ribs of an umbrella) instead of merely as supports for an expanded brim; and, as a necessary result of the change in the mechanics of the body, the central ring of the water vascular system has migrated from its original position about the gullet to an apical position in the center of the apical portion of the animal, equidistant from the border on every side.

The entire dissociation of the water vascular system from the mouth is the most difficult thing to explain in *Eldonia.* But, after all, this is not without a parallel. In the bilaterally symmetrical invertebrates one of the most fundamental structures is the nerve ring about the œsophagus, consisting of the supraœsophageal ganglion, the two circumœsophageal ganglionic connectives and the subœsophageal ganglion. The relationship of these nerves is entirely changed in the crinoids; here we find a circumœsophageal ring consisting of the supraœsophageal ganglion alone, the subœsophageal ganglion at the dorsal pole, with its continuation directly downward at right angles to the plane of the digestive canal instead of parallel to and directly beneath it, and the circumœsophageal ganglionic connectives resolved into numerous nerve

strands parallel to, instead of passing horizontally around, the gullet. Surely if such a fundamental rearrangement can take place in the nervous system we can not be surprised in seeing the water vascular system become entirely dissociated from the mouth.

Pelagic animals tend to become delicate and translucent, and if belonging to groups with a more or less calcified (or chitinous) skeleton, to reduce that skeleton to a minimum or to dispense with it entirely. Thus the entire absence of any trace of a skeleton in *Eldonia* does not prevent us from suggesting an affinity with the holothurians, more especially as the recent pelagic holothurian *Pelagothuria* has no trace whatever of calcareous elements.

Dr. Clark remarks that the oral tentacles of *Eldonia* are suggestive of the marginal clusters of *Lucernaria* and its allies, or perhaps are not fundamentally different from those of some rhizostomous medusæ. This would naturally be the case no matter to what group *Eldonia* belonged. The tentacles of *Eldonia* undoubtedly are subject to the same mechanical and physical forces as are those of the pelagic medusæ, and this would be amply sufficient to induce a strongly marked parallelism, no matter what their ultimate origin might have been.

The body of *Pelagothuria* is tubular, with the mouth at one end and the anal opening at the other; its alimentary canal is in loops (a long-drawn-out spiral); the swimming organ is merely an expansion of the oral disk. *Pelagothuria,* therefore, though similarly pelagic, is radically different from *Eldonia,* derived from a radically different stock.

The embryology and metamorphosis of the echinoderms lead us to believe that they were derived from phyllopod crustacean ancestry through the barnacles as a result of the sudden suppression of one half of the body and the consequent assumption of a circular body form. Since there are only two tentacles in *Eldonia,* we might suggest the remote possibility that *Eldonia* may have

arisen from a form like *Scytoplanes typicus* by a further sudden suppression of half of the body and the dropping out of three of the rays, the rest of the body curving about so as to form again a circular animal from one originally pentamerous, though ultimately derived from bilateral ancestors.

Louisella.—No marine animal is known except among the Elpidiidæ with a body form resembling that of *Louisella pedunculata.* A comparison between this fossil and such recent species as *Scotoplanes insignis* shows a similarity that can not but be more than superficial.

Dr. Clark in speaking of *Louisella* says that "none of the podia are sufficiently defined to enable one to make out even the form, let alone the structure, whereas if they were really like those of *Scotoplanes* and other elasipods, their rigidity would have caused them to be as well defined as any part of the body outline." Every one who has collected specimens of certain of the species of Elpidiidæ knows that they are as delicate and as difficult to preserve as are many, if not most, medusæ; even when hardened in alcohol the podia of such forms as *Deima pacificum* are extremely soft and flabby. If any species of the group adopted a pelagic habit this character would naturally be greatly accentuated.

Laggania.—It is difficult to see how *Laggania cambria* can be interpreted otherwise than as a holothurian of the elpidiid type, a form related to such species as *Benthodytes sanguinolenta,* or especially to *B. sibogæ.*

Circumstantial Evidence Suggesting the Possible Occurrence of the Elpidiidæ in the Palæozoic.—As I understand the three holothurians from the Middle Cambrian described by Dr. Walcott (*Eldonia, Laggania* and *Louisella*), they all fall within, or are closely related to, the family Elpidiidæ. Now the Elpidiidæ are preeminently creatures of the deep sea, and represent possibly the most strictly abyssal group to be found among marine organisms. The *Siboga* dredged one species in 31 fathoms, and the first species to be described was found in

50 fathoms in the Arctic Ocean; but the great majority of the species occur below 1,000 fathoms, extending downward to 2,900 fathoms.

Now in forms confined to the deep sea, or to exceedingly high latitudes, or subjected to widely varying temperatures or salinities, or occurring in highly saline, alkaline or acid water, or under unnatural conditions generally, the geological age of the maximum virility of the genera or families may be guessed by the amount of difference between the chemical and physical surroundings among which they now live, and the conditions obtaining slightly below low-tide mark on a tropical coast bathed by ocean water free from any admixture of fresh, and containing the normal proportion, in amount and in kind, of salts. Such forms as *Artemia,* occurring in salt pans, *Xiphosurus, Tachypleus* and *Carcinoscorpius* (*"Limulus"*) occurring in more or less foul and muddy situations, and the Elpidiidæ, characteristic of great depths, we therefore suspect of being relics of the earliest geologic times, representing what were once the dominant types in their respective groups, possessed of such vigor and adaptability that, forced by internal specific pressure, due to increase in the number of the individuals, they were able to accommodate themselves to these conditions. When these types began to wane new and vigorous forms arose in the tropical littoral which extirpated them from all the more desirable locations, allowing them to persist only in such unnatural situations as those into which they had intruded when in the prime of their vigor.

There is not the slightest reason for supposing that any markedly new animal type ever originated in the deep sea, or under conditions differing much from those found just below the low-water mark.

If we are ever to discover any recent representatives of such groups as the trilobites, the eurypterids, the blastoids or the cystids we shall find them not in the tropical or temperate littoral, but living under some highly ab-

normal conditions, in the deep sea, in highly saline, alkaline or acid water, in the regions of excessive cold or excessive heat (such as hot lakes), in stagnant pools in the ocean bed, in brackish underground lakes or streams, or in comparable situations; but apparently none of these groups were highly adaptable; though very abundant, they flourished through comparatively small extremes in their physical and chemical environment, from which subsequent vigorous types with the same or a greater economic radius promptly ousted them.

The disappearance of a group in a given horizon, it should be pointed out, does not at all mean that the group really vanished at that time; it means merely that at that time it disappeared from the littoral. Most groups undoubtedly persisted long after they ceased to occupy a habitat which is now a geological stratum, under locally unfavorable conditions, finally dying out at a time long subsequent to the last record in the rocks.

Not only does the deep-water habitat of the Elpidiidæ betoken a very ancient origin, but the group to-day is evidently senescent. The extraordinary shapes assumed by most of the species can only be interpreted as a result of an explosion of the characters induced by extreme age.

Thus, reasoning backward from a study of the recent fauna alone, we should expect to find the Elpidiidæ and *Artemia,* or very closely allied forms, in the early paleozoic rocks, representing the littoral in the age when they were at the height of their ascendancy, and we should be greatly surprised should they appear in any post-paleozoic formation.

Lorenzinia.—Lorenzinia, mentioned by Dr. Clark, is undoubtedly the cast of part of a medusa, as any one acquainted with the literature on the fossil medusæ can see.

Mackenzia.—The two specimens assigned to the genus *Mackenzia* appear to me to be undoubtedly mud-living actinians of the family Edwardsiidæ, closely related to

the *Edwardsia,* for the following reasons. In a semi-desiccated synaptid the longitudinal lines marking the longitudinal muscles become gradually obsolete, and the digestive tube, more or less distended with inorganic matter, becomes more and more prominent, so that finally we see an elongated worm-like object with a prominent digestive tube which bears a collar about the anterior end; longitudinal markings become obliterated and lost in the irregular foldings which take place, while these also obscure the other more flaccid internal organs; a soft mud-living actinian, on the other hand, is reinforced internally by numerous mesenteries; on desiccation these tend to lie flat, and to raise the body wall at the lines of attachment slightly, giving a fluted or pleated appearance, just as is shown in *Mackenzia.* No trace of a tubular digestive tube is visible in *Mackenzia,* nor is there any other internal differentiation, but there are prominent, regular and numerous parallel pleats; these pleats are four in number in the upper part of the body, but apparently five in the lower part, so that there are probably eight mesenteries represented; there appear to have been sixteen tentacles, two in each intermesenterial space; the contracted lower portion of the body suggests the physa of *Edwardsia;* it is probable, therefore, that *Mackenzia* is an actinian, and that it should be placed in the family Edwardsiidæ near the genus *Edwardsia.* Some of the preserved specimens of *Edwardsia farinacea* in the National Museum collection are almost identical with the specimen of *Mackenzia costalis* figured by Dr. Walcott, the similarity of the contracted anterior portion of the body being especially striking.

Systematic Position of the Genera Discussed.—When a biologist, especially a zoogeographer, undertakes to deal with fossils, he becomes of necessity somewhat of an iconoclast. The faunas of the several horizons represent to him not so many distinct and separate successive faunas each derived directly from that preceding, but so many distinct faunal regions, each equidistant

from the center, the center representing the phylogenetic starting point of organic life. In certain limited genera or in certain small groups an extraordinary progressive development is undoubtedly traceable through a greater or lesser extent of geologic time; but in general there is a balance between the organisms in each horizon which is strikingly similar to the balance between the organisms in every other horizon and between the organisms in each of the present faunal regions, so that, taking into consideration the circumstances under which the animals in each horizon lived, we are not able to say with any degree of accuracy that, phylogenetically speaking, any one fauna, zoogeographic or paleontologic, is *in toto* more primitive than any other.

Keeping this in mind and speaking solely as a biologist, I would suggest the following disposition of the genera described by Dr. Walcott:

Holothuroidea
- Family Elpidiidæ
  - Genus *Laggania*
  - Genus *Louisella*[4]
- Family Eldoniidæ (near the Elpidiidæ)
  - Genus *Eldonia*

Zoantharia
- Family Edwardsiidæ
  - Genus *Mackenzia*

Summary.—Eldonia is a free-swimming holothurian, and is most closely related to the species of the family Elpidiidæ.

In body form alone does *Eldonia* resemble a medusa; this general resemblance may therefore safely be disregarded as a parallelism resulting from a similar pelagic habit.

In the general shape of the body as well as in the course of the digestive tube *Eldonia* approaches *Trochosphæra* (and trochophore larvæ); but the enormous dis-

[4] Both of these genera can probably be referred, with a reasonable degree of probability, to subfamilies in this family; but it seems best to leave them, for the present at least, unassigned.

crepancy in size, the broad fringe about the body, the large tentacles on either side of the mouth, the absence of muscles of the group type characteristic of the rotifers, and the submarginal anus, seem to negative the idea that the two can be in any way related.

The medusoid body form, the absence of a protrusible proboscis and the presence of a large branched tentacle on either side of the mouth appear to offer conclusive evidence that *Eldonia* can not be a "worm."

The digestive tube of *Eldonia* resembles that of the heteroradiate echinoderms, and especially that of certain holothurians; the tentacles on either side of the mouth suggest an affinity with the holothurians; the radial canals, leading to a central ring, are comparable to the radial canals and the central ring of the holothurians; the broad circular muscle about the body suggests a modified longitudinal holothurian muscle, and is of the group type characteristic of the echinoderms; the broad brim about the body is strikingly similar to the brim developed in certain elpidiid holothurians, such as *Euphronides tanneri* and *Scytoplanes typicus*. A pelagic holothurian is known as an inhabitant of the recent seas; though very different in origin and in affinities from *Eldonia*, it demonstrates that a pelagic habit is not impossible in the group. The species of the family Elpidiidæ are preeminently inhabitants of the deep sea; this suggests that the fossil representatives of the family should be found in very early geological formations.

Therefore *Eldonia* is a pelagic holothurian, related to the species of the family Elpidiidæ.

No marine animals are known outside of the holothurian family Elpidiidæ which have a body form like that of *Louisella pedunculata* in all its details; but this species agrees in every particular with one or other of the species in that family. We can not, therefore, escape the conclusion that *Louisella pedunculata* should find a place in the family Elpidiidæ along with all the recent animals which in any way resemble it.

By exactly the same reasoning *Laggania cambria* is assigned to a position in the same group.

The type specimen of *Mackenzia costalis* shows a pleated structure which can only be interpreted as due to longitudinal mesenteries, probably eight in number; there appear to have been sixteen processes around the mouth which probably indicate tentacles retracted before preservation; the distal portion of the body resembles closely the distal portion of the body in the genus *Edwardsia*. Thus, as *Mackenzia costalis* presents characters not found outside of the Zoantharia, and in that group peculiar to the family Edwardsiidæ, it seems necessary to assign it to a position in the family Edwardsiidæ, near the genus *Edwardsia*.

SHORTER ARTICLES AND DISCUSSION

VIABILITY AND COUPLING IN DROSOPHILA

In the course of work done in the college year, 1911–12, under the direction of Dr. Castle, at the Harvard Zoological Laboratory, Cambridge, Mass., an experiment was performed to test the relative viability of the red-eyed and the white-eyed stock of *Drosophila ampelophila* Loew. The white-eyed race was obtained from Professor Morgan, while the red-eyed material was reared from banana exposed near the laboratory.

A large glass jar well supplied with fermenting banana and tightly covered with a double layer of closely woven cheese-cloth was used for the experiment. Five pairs of flies from the red-eyed stock and five pairs from the white-eyed stock were introduced on November 29, 1911. After a few weeks the jar was well supplied with flies of both eye-colors, but the red-eyes considerably surpassed the whites in number. Fresh food was introduced once and on February 12 a number of the flies were drawn off and counted.

Let us consider here what the expectation of the ratio between reds and whites would be, after the culture had been running indefinitely. Assuming equal viability of the two races, we should expect equality of reds and whites among the males, and three reds to one white among the females. This appears from the following combinations based upon Morgan's formulæ. The mutation producing white eyes, being recessive to the wild type, has been denoted by a small letter as suggested by Castle.[1]

Red female gives gametes x and x.
White female gives gametes wx and wx.
Red male gives gametes x and —.
White male gives gametes wx and —.
The combinations will then be as follows:

$$\left.\begin{array}{ll} 2wx\,{-}{-} = 2 \text{ white males}, & 1\ x\ \ x \\ 2x\ \ {-}{-} = 2 \text{ red males}, & 2\ wx\ x \end{array}\right\} = 3 \text{ red females},$$

$$1\ wx\ wx = 1 \text{ white female}.$$

[1] "Simplification of Mendelian Formulæ," AMERICAN NATURALIST, XLVII, 555, March, 1913.

It is evident upon inspection of these formulæ that although the red females have gained over the whites, this is due solely to the formation of two heterozygotes where at first we had a pure red and a pure white. Since the ratio of the three types of gametes does not change, we may expect the above recorded ratios of red and white flies to persist indefinitely.

Let us now observe the results of counts and compare these with the theoretical ratio. The count of February 12 gave 129 red males, 202 red females, 21 white males and 3 white females. Instead of equality in the males, we have 6 reds to 1 white, and instead of 3 to 1 in the females, we have 67 reds to 1 white.

On March 13 flies were again drawn off from the jar and counted, giving 303 red males, 514 red females, 36 white males and 2 white females. The males are now 8.42 reds to 1 white and the females 257 reds to 1 white.

On April 12 a count showed 1,341 red males, 1,363 red females, 95 white males and 24 white females, or 14.1 reds to 1 white among the males, and 56.8 reds to 1 white among the females.

In general these results show that the reds are outrunning the whites. Disregarding sex we expect a ratio of 5 reds to 3 whites to persist in the population. On February 12 we get 14 to 1; on March 13, 21.5 to 1 and on April 12, 22.7 to 1. On April 12 there are more white females than would be expected, an irregularity which can apparently be explained only by chance. The great excess of females in the first two counts probably denotes that the lethal factor clearly demonstrated by Morgan[2] was present in the stock and the equality of the sexes in the last count denotes that the lethal factor has been bred out.

Among the flies examined in the last count were a few reds in which the eyes were reduced to about one fourth the normal diameter, and also a spotted-eyed fly which was not counted in the numbers recorded. The latter had the right eye red with a white patch four ommatidia in diameter near the vertex, and the left eye white with a red spot eight to twelve ommatidia in diameter with a few smaller red spots below it near the posterior margin. Later examinations of the culture were made in the hope of obtaining a spotted-eye fly alive, but these were without success.

[2] "The Explanation of a New Sex Ratio in *Drosophila*," *Science*, N. S., XXXVI, 934, November, 1912.

Small-eyed flies were obtained from the same stock and further work is now being done with these.

The association of the differential factor between colored and white eyes, *w*, with the differential factor between long and miniature wings, *m*, was tested. Matings were made between white-shorts and red-longs, and between white-longs and red-shorts and in both cases the long-red female offspring were paired to short-white males. In this way the F_2 progeny gave directly a measure of the classes of gametes produced by the long-red F_1 females, except as they may have been affected by differences of viability. When white-shorts were mated with red-longs, the female offspring were of composition, *wmx—x*, giving excess of white-shorts and red-longs over the other two possible combinations; and when white-longs were mated with red-shorts, the female offspring were of composition, *wx—mx*, giving excess of white-longs and red-shorts.

Daughters of white-shorts by red-longs gave 3,371 red-longs, 1,136 red-shorts, 1,571 white-longs and 2,064 white-shorts.

Positive association of *w* and *m* is given by the equation

$$\frac{\text{red-longs} + \text{white-shorts}}{\text{red-shorts} + \text{white-longs}} = \frac{5,435}{2,707} = 2.$$

Greater viability of the longs is shown by the equation

$$\frac{\text{longs}}{\text{shorts}} = \frac{4,942}{3,200} = 1.54.$$

Greater viability of the reds is shown by the equation

$$\frac{\text{reds}}{\text{whites}} = \frac{4,507}{3,635} = 1.24.$$

Daughters of white-longs by red-shorts gave 1,047 red-longs, 1,116 red-shorts, 1,651 white-longs, 671 white-shorts.

Negative association of *w* and *m* is given by the equation

$$\frac{\text{red-longs} + \text{white-shorts}}{\text{red-shorts} + \text{white-longs}} = \frac{1,718}{2,767} = 0.62.$$

According to previous work on these factors this equation should have given 0.50, and we may suppose that larger numbers would have corrected this discrepancy.

Greater viability of the longs is shown by the equation

$$\frac{\text{longs}}{\text{shorts}} = \frac{2,698}{1,787} = 1.51.$$

In this case the whites appear in excess of the reds.

$$\frac{\text{reds}}{\text{whites}} = \frac{2{,}163}{2{,}322} = 0.931.$$

Dividing the sum of all the reds bred by the sum of all the whites bred we get an excess of reds—6,670 : 5,957 = 1.12.

These counts add nothing new to the theory of association, but are in agreement with Morgan's ratios.

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A DISCUSSION OF THE RESULTS OBTAINED BY CROSSING ZEA MAIS L. (MAIS DJAGOENG) (—REANA LUXURIANS DUR.—TEOSINTE) AND EUCHLÆNA MEXICANA SCHRAD[1]

THE author prefaces his discussion of the hybrids of maize and teosinte with a minute study of the male and female spikelets of both plants, showing the similarity between them.

After reviewing the work of Harshberger with the cross maize ♂ × teosinte ♀, he takes up the result of his own reciprocal cross, maize ♀ × teosinte ♂. He shows that the first generation hybrids by the latter cross were uniform and agree closely with those from the reciprocal cross made by Harshberger.

The plants of the second hybrid generation of the cross, maize ♀ × teosinte ♂ form a diverse series, of which the different individuals differ widely in stooling and branching ability, as well as in the structure of the ear. A complete reversion, however, to either one of the parent types never occurs. The series tends more towards the maize than the teosinte type, and it is shown that associated with the stronger development of the maize type, is a reduction in the number of branches, a reduction in the number of ears per plant, a less horny texture of the axis and of the calyx-glumes, and a reduction in the depth of the pits of the axis. The nature of the diversity in the second hybrid generation argues against the absolute purity of the sex cells.

[1] "A Discussion of the Results Obtained by Crossing *Zea mais* L. (*Mais Djagoeng*) (*-Reana luxurians* Dur. *-teosinte*) and *Euchlæna mexicana* Schrad," by J. E. van der Stok, in *Teysmannia*, Vol. 21, 1910, p. 47–59. The translation upon which this abstract is based was made by Karle Lotsy, Bureau of Plant Industry, U. S. Dept. of Agriculture, Washington, D. C.

Another cross was made with two varieties of Java maize, Madoera and Menado, using pollen from the first hybrid of the maize × teosinte cross. The resulting plants varied widely regarding the stooling ability and structure of the ears. This is not surprising in view of the inequality of the sex cells of the hybrid.

Seed from the second generation hybrids were sown and that again from the resulting plants, thus securing fourth generation hybrids. These hybrids (fourth generation) while differing widely from each other, remained within the limits of the most different types which appeared in the second generation hybrids. The practical result of these crosses, maize × teosinte, are not very satisfying. The resulting hybrids are far inferior to teosinte for fodder, and although the seed can be more easily harvested from the hybrids than from teosinte, it is not nearly so valuable as that from good varieties of maize.

The author closes by calling attention to the fact that teosinte is immune from the chlorosis disease of maize which is very prevalent in Java, but the hybrids of maize and teosinte showed no decrease in sensitiveness to the disease.

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